Papers on

NEW ZEALAND ECHINODERMS

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The Direct Development of a New Zealand Ophiuroid

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The Direct Development of a New Zealand Ophiuroid.

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I. Introduction.

In 1916 Professor H. B. Kirk published in the 'Transactions of the New Zealand Institute', vol. 48, a preliminary notice 'On the much abbreviated development of a Sand-star (*Ophionereis schayeri*?)'. In that paper he briefly recorded having discovered on stones at Island Bay some clusters of eggs, from which, later, young ophiuroids began to emerge. The measurements of the eggs are given, with a description of the hatching process, and notes on the newly emerged stars. He expressed his belief that the development was absolutely direct, but could not then speak with certainty. Owing to the opacity of the embryo no internal structure was observable, sectioning being the only process likely to give satisfactory results, and this could not be done at the time for lack of sufficient material. Various circumstances having prevented Professor Kirk's continuation

with this remarkable case, the work described in the present paper was undertaken by the writer.

This paper covers the general embryology from the first cleavage of the fertilized egg to the stage of the young sand-star of seven arm-segments. The early formation of the rudiments of the oral skeleton is treated in some detail. The development of the nervous system and reproductive organs is not included.

The more remarkable facts which have emerged from this study are, briefly: the egg, which is heavily yolked and pigmented, divides to form a blastula with a small and eccentric blastocoel. Invagination is very largely replaced by epiboly, the archenteron being a transient feature and giving rise to no structures. There is no larval stage. The coelom arises late by splitting in mesenchyme, and the definitive gut by a hollowing out of a solid mass of hypoblast. A young, pentagonal ophiuroid emerges from the egg membrane, and begins active movement with the aid of functional podia.

The extraordinary fact that the coelom arises by splitting in mesenchyme, and not, as usually occurs in Echinoderms, by derivation from paired pouches of the archenteron, will be seen to bear interesting comparison with a similar process recorded in a paper by A. Russo on the embryology of the viviparous ophiuroid Amphiura squamata, published in the 'Atti della R. Academia delle Scienze Fisiche e Matematiche' of Naples in 1891. I should note that Russo's paper did not reach me till I had already formed my conclusions on this matter. Russo's deductions have been made the subject of unfavourable criticism, though no one appears to have actually demonstrated that the statements were unjustified. That the present species should behave in a like manner to that studied by Russo would seem to render necessary a reinvestigation of his work.[1] In any case, it is clear from the present instance that our ideas on Ophiuroid, and indeed Echinoderm, embryology cannot be confined within the Recapitulationist scheme in its narrower form. The total absence of any larval stage or vestigial larval form is believed to be unique among Echinoderms—at least among those whose development has been described. The possibility

[1] The writer is now engaged on this work.

that such may be the case in other unrecorded instances now becomes evident.

The difficulties in the matter of identifying the ophiuroid will be discussed in a later section of this paper (p. 382).

The material upon which the present work has been based was all collected at Island Bay, Wellington, partly during the breeding seasons (late August) of the years 1936–8, and partly during 1915–27, for which latter material I am indebted to Professor Kirk.

The plates were drawn either with the aid of a projection-prism or of a camera lucida, or, when polarized light was used and where the illumination was faint, with a squared eyepiece.

To Professor H. B. Kirk, of Victoria University College, Wellington, New Zealand, I have to express my gratitude for his interest in the work, both in the field and laboratory; also for the free access to his observations recorded subsequently to the publication of his 1916 paper. These latter are acknowledged in the text as they occur. To Mr. C. E. Palmer also I tender my thanks.

I am grateful to Professor E. S. Goodrich for advice on the terminology employed in regard to the germ-layers. A great deal of confusion has arisen owing to the premature application by some authors of the terms 'epiblast', 'hypoblast', and 'mesoblast' to groups of more or less indifferent cells, merely because of the position that they happen temporarily to occupy. Thus, in this paper, cells of the outer zone (micromeres) which later contribute to the wall of the archenteron are not regarded as epiblastic. Similarly, that inner germ-layer that gives rise to both mesoblast and hypoblast is here referred to as 'mes-hypoblast'.

II. Ophiuroid Embryology.

Although a very large number of larval forms of Ophiuroids have been described and figured (the parent species often being unknown), comparatively little work has been done covering the entire embryologies of individual species of ophiuroids.

MacBride in 1914 could enumerate only three species whose development was known—namely, Ophiothrix fragilis,

Ophiura brevispina, and Amphiura squamata. MacBride himself indicated that he placed little credence in the account of Amphiura, and thus only two embryologies are described in his text-book. On this minimum of material the general theory of ophiuroid development is formulated. Amphiura, as described by Russo, does not conform to this theory. It is dismissed from further consideration in the following words: 'Russo (1891) has given a general account of its development, but as this worker did not employ the method of sections to any great extent, and as the young stages are met with seldom and are very opaque, it is quite likely that his account is inaccurate. According to Russo, the blastula is converted into a two-layered gastrula by delamination (!)[1], each cell dividing into an inner endodermic and an outer ectodermic portion, and the coelom is said to arise as splits in a mass of mesenchyme. Such statements as these are improbable in the highest degree.'

In vertebrate embryology it is a well-known fact that the presence of a yolk mass has frequently a most powerful modifying influence on development, especially on the earliest cell divisions and on the gastrulation. The embryo of Amphiura is stated to be densely pigmented. As pigment in Ophiuroid eggs is, so far as known, generally associated with yolk, I presume this is the case in Amphiura.[2]

Amphiura squamata differs from Ophiura and Ophiothrix in being viviparous. For an illustration of the profound effect that viviparity can exert on the ontogeny of an organism, the mammals may be cited. Of course, viviparity in the case of Amphiura squamata is not so complete as in the Eutheria; but, nevertheless, there is an 'umbilical' attachment to the parent during part of the development (Fewkes, 1887). Therefore it should not be a matter for disbelief that the early stages of this animal, as described by Russo and Apostolides, are different from those of Ophiothrix and Ophiura. As the

[1] Apostolides (1882) had already recorded this fact. Fewkes (1887) independently suggested that delamination might occur.

[2] Since the above was written, I have had the opportunity of examining the egg of Amphiura squamata and find it is in fact heavily yolked.

present writer has not had the opportunity yet for studying Amphiura for himself, it is not intended here to assert that Russo's account of Amphiura is true (see note to p. 378). But it is urged that the summary dismissal from consideration of his account is at least unjustified.

In the species studied by the writer the extraordinary resemblances of certain of the developmental processes to those described by Russo in 1891 became increasingly evident during the progress of the work. In both cases the egg is heavily pigmented, in the present case pink or buff, in Amphiura squamata, 'rossastro' (Russo, 1891). In the present case, and probably in Amphiura also, the pigment is associated with a yolk mass. In both, the early cleavages are similarly irregular, and the blastocoel is small. There is no free-living, bilateral, larval stage. In both cases the coelom arises by splitting in a mesenchyme mass. The only important difference is that in Amphiura Russo states that the primary germ layers arise by delamination, whereas in the present instance they arise by a very reduced form of invagination, accompanied by an extensive process of epiboly. Further, the bilateral larval stage is entirely suppressed in the present form, whereas a reduced larva persists (within the egg) in Amphiura.

In the case of the other two Ophiuroids whose developments had been described, the processes follow those observed in most echinoderms, typical blastulae and gastrulae forming, and the coelomic cavities being derived from the enteron by the formation of pouches. Ophiura, whose development was worked out by Grave (1900), has a yolky egg and a much modified larva. This takes no nourishment, but creeps about on the bottom. It then metamorphoses into the radially symmetrical ophiuroid. Ophiothrix, described by MacBride, develops into the typical Ophiopluteus larva, which is pelagic for a while, and then metamorphoses and sinks.

The fact that in Ophiura a 'much modified', 'worm-like' larva is produced from a yolky egg is surely significant. Are not further modifications highly conceivable as the influence of the yolk mass increases?

The present species is compared in greater detail with

Amphiura, Ophiura, and Ophiothrix in a later section of this paper (p. 431). This preliminary note is intended only to indicate the rather unsatisfactory condition of our knowledge of ophiuroid embryology. When, later in the paper, the development of the skeletal system is described, a further series of conflicting accounts is brought together, and considered in the light of evidence provided by the present species.

III. Identity of the Species.

When Kirk (1916) published his paper he provisionally suggested that the eggs could be referred to Ophionereis schayeri, that being the commonest species at Island Bay; also, he considered that the terminal plate of the young ophiuroid resembled that of Ophionereis. Mortensen (1924) comments as follows on this deduction:

'Grave objections may be raised to the referring of these eggs and embryos to Ophionereis fasciata (= Ophionereis schayeri). Above all, the eggs of this species are very small, about 0·1 mm., while the eggs observed by Kirk were 0·5 mm. This small size of the eggs in Ophionereis fasciata almost certainly indicates that it has typical pelagic larvae, not direct development. Further, Kirk states that the tube feet of the young ophiuroids were provided with a number of bristle-like processes,[1] but the tube feet of Ophionereis fasciata are perfectly smooth.'

However, shortly after the appearance of the 1916 paper, Kirk was convinced from examination of Ophionereis fasciata that the eggs did not belong to that species. Shortly afterwards he made the following observation, which he has communicated to me, leading him to the conclusion that the species concerned was probably Pectinura cylindrica. As it has not yet been recorded in a published paper, Mortensen was, of course, unaware of it in 1924, when he wrote the above criticism.

Some specimens of the species concerned had been reared by Kirk in an aquarium tank. When, after some weeks, all the

[1] The present writer believes these must have been artifacts, perhaps crystals, as they do not occur in his specimens.

embryos appeared to have died, no further notice was taken of the tank for a year or so. Then, when the tank was being cleared out in preparation for another purpose, a single half-grown ophiuroid was discovered, and identified as Pectinura cylindrica, by Mr. H. Farquhar. Two possibilities thus are open—either the ophiuroid was a survivor of the original batch of embryos, or had been accidentally introduced into the tank.

In order to identify the eggs, I kept a close watch on the breeding grounds over the few weeks of August immediately prior to the deposition of the eggs, during 1937 and 1938. In 1937 the observations were upset at the critical period by a heavy southerly gale which rendered the situation inaccessible. When eventually I could wade out, it was to find the eggs already laid and fertilized. Numerous specimens of Ophionereis were observed and also two specimens of Pectinura cylindrica. The gonads of these latter when examined proved to be very small, and led me to suspect that a recent evacuation had occurred. A similar watch was kept on the spawning ground in August of the present year (1938), but although I collected eggs which could not have been laid more than a few hours or so, no sign of any species other than Ophionereis fasciata was observed. An earlier attempt to keep Pectinura cylindrica adults alive in the laboratory did not succeed, although Ophionereis and the starfish Asterina appeared to thrive in the same tank and at the same time.

In view of the above observation of Kirk, I had assumed that the species was fairly probably Pectinura cylindrica, but it has only recently come to my notice that Farquhar (1898) had established that this latter species is viviparous. This has been confirmed by Th. Mortensen (1925), who has also shown that the same applies to the very closely allied form Pectinura gracilis. The only other species of Pectinura known to occur in New Zealand waters is Pectinura maculata, a large form, occurring at a depth of about twenty feet off the coast of Wellington. In April of this year (1938) the writer examined specimens of this species dredged off Wellington Harbour Heads by Mr. A. P. Oliver. The gonads were obviously nearly ripe, and very large. This species is not hermaphrodite. The eggs re-

sembled in general appearance those of the present unidentified species, but were slightly larger, measuring from 0·56 to 0·625 mm. while still contained within the gonad,[1] whereas the eggs of the present species do not exceed 0·5 mm. when fully developed and laid. It is possible that a diminution in volume could result from maturation, by the expulsion of fluid. However, the disparity between the spawning periods still presents a difficulty as it seems unlikely that Pectinura maculata would carry such developed gonads from March till August before depositing the eggs and sperm, and further it is improbable that Pectinura maculata could oviposit in some of the places we have seen.

The writer has not been able to find the other species mentioned by Mortensen (1924) as occurring in the same situations as the present eggs are found—certainly the three species which I have investigated (namely Ophionereis, and the two Pectinuras, Pectinura cylindrica and Pectinura maculata) are the only ones commonly met with in the locality where the unidentified eggs are found; and the regular occurrence of the eggs in that situation for the last twenty years at least would indicate that the parent cannot be any spasmodically visiting species.

It is therefore concluded that the eggs are laid by a species inhabiting the deeper waters off the coast of Cook Strait, and coming up to the tidal zone to spawn, apparently returning to the deeper water immediately the eggs are deposited.

The following species are ruled out from consideration: Pectinura cylindrica, Pectinura gracilis, Pectinura maculata, and Ophionereis fasciata, all of these occurring in the vicinity.

Further investigation is obviously required. In the meantime there is no justification, in the writer's view, in naming the ophiuroid on the assumption that it is a new species. It would seem preferable to refer to it by some such term as 'Kirk's ophiuroid' till the question of its identity is settled.

[1] Prof. Kirk has since communicated to me that the mature eggs of Pectinura maculata are much larger.

IV. Laboratory Methods and Technique.

1. Rearing of Specimens.

For the rearing of specimens two rectangular glass aquarium tanks were used, one of about ten litres capacity, the other of twenty-five litres. These were covered to help prevent evaporation, and could be shaded from light when required. The two tanks were used in conjunction with an automatic rocking apparatus.

Aeration of the water was obtained by periodically introducing small stones covered with coralline seaweed—this type being chosen as less likely to harbour undesirable predacious worms, &c., and having only a very slight mucilaginous secretion.

With the above treatment one of these tanks has supported a healthy growth for a period of two years' continuous use.

The apparatus described does not lend itself to detailed observation of any single embryo or group of embryos, and to meet this requirement the following 'set-up' was used:

A group of embryos within their capsules, and oriented in a known direction, is placed in the small watch-glass A. The latter is itself placed in a Petri dish B containing sea-water, to completely cover the watch-glass. By means of siphon cords passing between the upper and lower reservoirs of sea-water a slow but steady circulation of sea-water takes place. The Petri dish B is itself placed in a larger Petri dish C and the space between the two is occupied by wet cotton wool; the evaporation from the latter keeps the embryos at a comparatively uniform and natural temperature—which is observed by a thermometer. The Petri dishes are set on the stage of a dissecting microscope so that the embryos can be readily observed without interference. The whole mount is placed within a large glass bell-jar.

With this 'set-up' a fairly uniform environment at a temperature of 13·5–15° C. was obtained despite considerable variation in the general atmospheric conditions of the laboratory, while at the same time drawings and observations could be made whenever required. The smaller dish A is a safeguard

against any mishap to the siphon system, and precludes the possibility of the embryos being exposed to the air.

As the normal breeding ground of this species is sufficiently near to low-water mark to be appreciably subjected to changes of atmospheric temperature, it was not considered that the variation of 1·5° C. indicated above could have any ill effect.

2. Narcotization and Fixation.

Anaesthesia of the motile stages preparatory to fixation was obtained easily and gently by placing a number of the animals to be treated in a Petri dish of sea-water about three inches in diameter, and dropping on the surface of the water a single crystal of chloral hydrate. Chloroform and ether were found to have too violent a reaction, causing spasmodic contractions. Subjecting young motile stages to strong light has an effect resembling anaesthesia, but I have never used this as a regular method to this end.

Embryos and narcotized young forms were fixed in Zenker's bichromate-mercuric chloride fluid without acetic acid, and in Bouin's fluid. Owing to their small size, twenty minutes to half an hour was found quite sufficient.

3. Whole Mounts.

Owing to the excessive opacity of the embryonic stages, only the earliest cleavages make satisfactory whole mounts. No bleaching reagent was found which could remove the pigment; the latter is closely associated with the yolk, and accompanies the yolk in its later movements. However, whole mounts of the young animal after it has reached the pentagonal disc stage are very instructive, and have been largely used. Even here, however, the dense pigments survive till the animal is some weeks old, and until their disappearance staining is undesirable. Stages which have lost the pigmentation were best stained with carmine, this bringing out the ambulacral system particularly well. For study of the skeleton no stains should be used.

4. Sectioning, Imbedding, and Orientation.

A number of difficulties were encountered here.

The egg has a tough, transparent egg-membrane of the con-

sistency of fine chitin. It was found that as the material was passed through the reagents this membrane tended to contract more and more on to the developing embryo, compressing and indenting its surface. The method was employed of first softening the membrane with Eau de Javelle, immediately after the fixation, and then passing the egg through the reagents. While collapse of the membrane still occurred it was less disfiguring.

The abundance of yolk in the egg renders it very brittle; this becomes greatly aggravated if the treatment in xylol exceeds an hour or so. In actual practice I found I could safely remove an egg from the xylol baths after only about two minutes.

The minute size of the egg made necessary special methods for imbedding in order to obtain a desired orientation. The double-imbedding method of Newth (1919) when employed was found unsuitable, as the differential contraction of the celloidin and wax precluded cutting very thin sections—and thin sections were often found necessary. Accordingly the method of double imbedding was employed, using two paraffin blocks in place of one of celloidin and one of paraffin.

5. Staining of Sections.

The later stages, in which the yolk has been largely absorbed or localized in the gut-wall, were found to stain excellently in Mallory's triple stain. Haematoxylin was also used. But the earlier stages offered a great difficulty owing to the density of the yolk granules which are intensely basiphilic. Thus the yolk granules cannot be certainly distinguished from nuclei as the former structures stain deeply with nuclear stains and mask the true nuclei. Various solvents were employed in an attempt to dissolve out the yolk, but none was found which did not also attack the protoplasm. Finally, for those stages of the egg which are obscured in this way by the yolk, I was forced to use the following methods—which gave fairly satisfactory results:

It was found (by accident) that if a section through a blastula in which the cells are still fairly large (the number being not more than 500 or so) were treated with Mallory's triple stain the individual cells became visible owing to the fact that the aniline blue stained the faint intercellular secretions, while the methyl

orange and Fuchsin stained only the cells themselves and their contents. Nuclei and yolk grains, of course, were indistinguishable, but the importance of the nuclei for my immediate purpose was reduced because the positions of cells could be ascertained independently by their outlines. The method was found applicable to gastrulae also and to the later stages, owing to various peculiarities in staining properties of the germ layers. For instance, epiblast proved to have a stronger tendency to stain with methyl orange than did the hypoblast. Also the boundary between epiblast and hypoblast is marked by a blue line—indicating an intercellular mucilaginous secretion. The fluid of the blastocoel when coagulated readily takes the aniline blue, and thus the blastocoel can be traced easily through its various phases till its complete obliteration. The affinity of the epiblast cells for methyl orange proved invaluable in tracing the epibolic inwandering of cells which occurs during the formation of the gastrula.

A method was later found (also accidentally) by which the nuclei could be clearly demonstrated, though only temporarily, as the preparation soon changes. It is as follows: thick sections (about 16μ) are required. They are immersed for a few minutes in aniline blue, and then transferred to Fuchsin where they are left for a few moments and then rinsed and examined quickly while wet. The nuclei show up blue, the cytoplasm pink. This effect is obviously caused by the fact that in thick sections the nuclear membranes are in many cases undamaged. Thus, when the section is immersed in aniline blue, this stain penetrates the nuclear membrane; when the sections are transferred to Fuchsin, the cytoplasm, being exposed, readily yields up its blue stain, and becomes pink, but those nuclei which have their membranes intact remain blue for a short period until the aniline stain has time to diffuse out.

I am interested to note that Dr. Th. Mortensen (1920) records a rather similar difficulty in the case of the crinoid Antedon petasus of Scandinavian seas. He apparently found no solution.

For studying the distribution of yolk iron haematoxylin (Heidenhain's) was used, this staining the granules an intense black.

6. Mapping of Cavities and Structures.

Owing to the opacity of the young animal at the time when the coelom and definitive gut are being excavated, it is not possible at that stage to obtain a general view of the body cavities in whole mounts. Sectioning is the only process. Where the cavities form an extensive system, as in the case of the hydrocoel, it is difficult to visualize their form and extension simply by looking through a series of sections from one end of the animal to the other. One method, a long one, by which such structures can be studied, is to construct a model—from wax, paper, or plasticene—copying each section on an enlarged scale and then superimposing them one on another in their correct relative positions; the model can then be dissected and examined.

To obviate the large expenditure and time which the above process entails, a projection method was devised and, provided care was taken, gave good results. This did not give a three-dimensional model, but a projection on to any required plane of space of the structures and cavities of such a three-dimensional model. As a description of a method essentially the same as that employed by the writer has recently been published by Pusey, 1939, there is no need to describe it here (see List of References).

7. Examination of the Skeleton in Young Forms.

For the study of the development of the calcareous plates the use of polarized light has proved invaluable. Under ordinary light the plates are difficult to observe in their early stages owing to their extreme transparency. Efficient clearing is essential for this purpose, and no staining is required. As the skeletal plates of Echinoderms are anisotropic, being each composed of a single calcite crystal, they show up brilliantly with a glowing, golden light under crossed nicols, the fleshy parts remaining invisible in a dark field. I believe that this method has not been systematically employed before in Ophiuroid development; at all events, its use has cleared up certain points which had been left in doubt in the literature available to me in

New Zealand. Further discussion of the use of polarized light in connexion with the developing skeleton is reserved to the section of this paper dealing with that phase.

8. The Skeleton of Older Forms.

While the previous method was useful for young ophiuroids, for the older and thicker stages it was found necessary to remove the fleshy parts. Owing to its complex nature, dissection is extremely difficult. Various solvents were experimented with, including digestive enzymes,[1] but finally the following simple method was found which gave excellent results:

The animal was placed in a small Petri dish, and about fifty times its volume of 10 per cent. potassium hydroxide added. This was placed in an oven and left till evaporated. This process was repeated till all the soft parts were dissolved away. With due care being taken, the ossicles then lay in their relative positions on the floor of the dish. By gently pouring in melted wax and allowing it time to pass between the ossicles without permeating them, and then cooling, the skeleton could be removed in one block, its elements still preserving their relative positions. A slide was then thickly coated on one side with gum acacia, and the block placed on it so that the gum moistened the side formerly in contact with the floor of the Petri dish, and on which, consequently, the ossicles were exposed. The preparation was then left to dry, care being taken that the gum was sufficient to impregnate and firmly fix each ossicle. Then the wax was removed by heat and xylol, leaving the complete skeleton exposed on the slide.

If the preparation be now mounted in Canada balsam, the ambulacral canals within the ossicles come into view.

V. Spawning.

1. Situation.

The locality which is regularly chosen for the deposition of the eggs is characterized by its very rocky coast-line. It is

[1] Pepsin is, of course, prohibited owing to an acid medium being necessary.

situated on the small headland which separates Island Bay and Ohiro Bay, Wellington, on the northern shore of Cook Strait, and exposed to southerly gales. The eggs are found attached to small stones, generally underneath them, though Kirk records finding them also on the sides. Sometimes they are attached to crevices on the larger rock masses, and occasionally are found on a species of encrusting seaweed of gelatinous texture. They are laid in groups of from a score to a hundred or more, the egg membranes being in close contact, and sometimes tending to adopt a honeycomb pattern through lateral compression. The egg groups form flat expansions generally one deep, but sometimes two or three deep. The eggs are so placed that at maximum low tide they are covered by only about twelve inches of water. When the weather is bad, as is not infrequent at that time of year, the seas are very rough indeed, and the eggs must be disturbed by the breakers.

2. Time of Spawning.

The eggs are laid by the parents at, or near to, the time of high tide, but it is not possible to obtain them till the following low tide, six hours later. Spawning takes place in the latter half of August, usually about the 20th, but sometimes as much as a week earlier. Professor Kirk has kindly communicated his records of years 1916, 1917, 1919, and 1928. To these are added my observations for 1936, 1937, and 1938. Spawning was abnormally early in 1916 and 1919. In an endeavour to find the factors controlling the date of spawning reference has been made to the Meteorological records of the Wellington Observatory for the years concerned, and to the dates of full moon (as providing an index to the tides). It was found that no relationship could be observed between the date of spawning and the meteorological data given. It would therefore seem that the immediate controlling factors must be purely local variations, perhaps influenced by local winds or storms, perhaps by variations of a purely submarine character.

I am indebted to the late Dr. Kidson for the meteorological data.

In reading the literature dealing with Northern forms, I was

surprised to notice that in every instance in which the time of breeding of an ophiuroid was given it was either in or near August. Dr. Th. Mortensen (1929) records that he found the larva of Ophiura affinis at Kristineberg 'on one of the first days of August' (1919). He also states of Amphiura filiformis that the larva is found at Kristineberg 'at least from the later part of July until the middle of September'. Professor Graham Kerr records having taken ophiuroid larvae off the coast of Britain in August. J. W. Fewkes (1887) states that the young are found in the bursae of Amphiura squamata at Newport, U.S.A., in August and September, but does not make it clear if those are the only months.

This being so, it seems very curious that the present species should also choose August for its breeding time, seeing that the corresponding season in the Southern Hemisphere is February. There is no record of anyone having found the eggs of this species in February, so the possibility that this species breeds twice a year seems ruled out.

VI. General Embryology from the First Cleavage to the Formation of the Coelom.

1. The General Characters of the Egg.

Kirk (1916) thus describes the egg:

'The eggs are spherical, 0·5 mm. in diameter, each with a perfectly transparent, thin, but extremely tough chitinous envelope. They are deposited in irregular clusters of 10 to 100 or more. The embryo does not occupy the whole of the space within the envelope, but is surrounded by colourless, apparently mucilaginous matter. The envelope was so tough that I could not tear it away satisfactorily, the embryo getting crushed in the process. The embryo is of a buff or pinkish brown colour, and is so opaque that no internal structure is to be observed. The pigment is very refractive to all ordinary solvents. For knowledge of internal structure sectioning is likely to be the only process, and for this I shall have to obtain fresh material next year.'

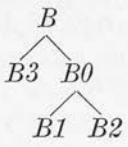
2. From the First Cleavage to the Morula.

The earliest stage observed was that of the first cleavage. In this stage a curious irregularity is to be noted in the relative sizes of the two first blastomeres. These may either be equal in size, as occurs in about two-thirds of the embryos, or markedly unequal, as occurs in the remaining third. When the former is the case (fig. 1, Pl. 20) the second cleavage follows in the normal way, at right angles to the first, and divides the egg into four approximately equal blastomeres. Stages of this process are shown in figs. 1–4, Pl. 20, drawn from living embryos. It will be noted that the first indications of the second cleavage take the form of a constriction round each of the two blastomeres, deepening earlier on the inner side than on the outer. During the stage of two blastomeres, and for the earlier part of the stage of four blastomeres, the opposed faces of the blastomeres are plane, the cells being in close contact; but during the latter part of the four-cell stage the blastomeres assume a rather more nearly spherical form and consequently become slightly separated by a space in the middle (fig. 4, Pl. 20).

When, however, the first cleavage is unequal a different plan of division appears to follow. I have not been able to observe in life the process of cleavage when the blastomeres are unequal, but the following series of stages studied in preserved material seems to indicate how the four-cell stage is arrived at. The unequal first cleavage (fig. 6, Pl. 20) presents two blastomeres similar in colour and density, but one about twice the size of the other. Their opposed surfaces are in contact and plane. Another specimen which appears to follow on the first unequal cleavage is shown in fig. 7, Pl. 20 of the same plate. A single blastomere *A* is accompanied by three rather smaller blastomeres, the latter grouped in such a way as to suggest their origin from *B*, the larger blastomere of the unequal first cleavage. In the figure, the cell numbered *B3* has a plane wall passing from the centre to the periphery, whereas cells *B2* and *B1* are separated by a wall which passes from the periphery to the wall of *B3*. This seems almost certainly to indicate that *B3* was cut off first from the original large blastomere, while *B1* and *B2*

were derived from a subsequent cleavage of the remaining cell. The cell lineage thus would be:

First cleavage (2 cells) *A*
Second cleavage (3 cells)
First stage
Second cleavage (4 cells)
Second stage



A, *B3*, *B1*, and *B2* being the cells which comprise the four-cell stage, arrived at by three separate cleavages.

The net result of this plan of division is similar to that which follows when the first cleavage is regular, the four blastomeres being approximately equal in size. This point is further discussed on p. 431, where it is compared with a somewhat similar plan of cleavage described by Apostolides and Russo for the Ophiuroid Amphiura squamata.

A study of sections through the blastomeres of the first cleavage reveals no visible qualitative distribution of cytoplasm. In each blastomere there is a peripheral narrow zone comparatively free from cytoplasmic products, and a central and extensive zone occupied by cytoplasm heavily laden with yolk granules and pigment. No definite polar bodies have been observed by the writer.

As explained earlier in the paper, study of the nucleus in the earlier stages is precluded by its feeble staining properties and the density of the yolk granules which are intensely basiphilic, and thus mask any true chromatin matter.

Polarity and Prelocalization.—When the third cleavage takes place two important new features become observable—namely, (1) the polarity of the egg, and (2) the fact that a prelocalization had occurred during the four-cell stage. This cleavage, which is horizontal, results in the formation of an eight-cell embryo, the blastomeres of which are arranged in two quartets (figs. 5, 11, and 12, Pl. 20). The upper quartet comprises cells of barely half the size of the lower quartet. The upper group, micromeres, occupy the animal pole of the egg, and the lower group, macromeres, occupy the vegetal pole—as is shown by the later development. That this cleavage should be differential both quantitatively and qualitatively indicates

that at least in the four-cell stage, and perhaps earlier, a prelocalization must have occurred. Unlike the case of Paracentrotus described by Boveri and quoted by Wilson (1928), this prelocalization cannot be correlated with pigment distribution, for all the blastomeres are at this stage equally densely pigmented, and are similarly provided with yolk.

Although no experimental embryology was attempted in the present instance, it was noted that in cases where eggs had been accidentally damaged, and the blastomeres separated, no further development took place. This is contrary to the usual totipotence of Echinoderm blastomeres, and is probably related to the large proportion of inert yolk present. In cases where blastomeres were ruptured, the portions of protoplasm rounded up in the usual way to form spherical masses, but no further development took place, and degeneration ensued on the following day.

The cleavages which follow the eight-cell stage become irregular, and 'out of step'. In a group of eggs kept under observation at this period it was noted that a sliding of the blastomeres occurred, the general conformation of the blastomeres changing quite apart from the alteration produced by the cleavages themselves. In the stage corresponding approximately to the thirty-two-cell stage of other echinoderms (fig. 13, Pl. 20) the embryo is a morula, no observable blastocoel being present. The difference in size between the micromeres and macromeres is much less marked, but still readily observable. The outer blastomeres are markedly turgid, each being approximately spherical. At the stage of about sixty-four cells the embryo still is a morula, but the cells are notably less turgid, having plane walls where they abut on their neighbours.

Rate of Cleavage.—During the 19th and 20th August 1938 a group of eggs was kept under constant observation for twenty-three hours covering the development from the two-cell stage to the morula (when observations were discontinued through fatigue). The following extracts from the laboratory log show the time relationships for the early cleavages.

Note: The eggs were not more than six hours old when collected.

Time.	*No. of hours after time of collecting.*	*Stage.*
4.30 p.m.	½ hour.	Two cells.
5.00 ,,	1 ,,	Dividing.
5.30 ,,	1½ ,,	Mostly four cells, some still dividing.
6.00 ,,	2 ,,	Four cells; separated still by flat planes.
7.00 ,,	3 ,,	Four cells: cells rounded off.
7.45 ,,	3¾ ,,	Dividing: cells marked by transverse furrows.
8.00 ,,	4 ,,	Eight cells.
8.45 ,,	4¾ ,,	8–12 cells
9.30 ,,	5½ ,,	About 16 cells: cleavages becoming irregular.
10.00 ,,	6 ,,	Several cells furrowed.
11.00 ,,	7 ,,	Several cells furrowed or dividing Morula.
12.00 midnight	8 ,,	Over 20 cells Morula.
2.00 a.m.	10 ,,	Morula: about 32 cells.
4.00 ,,	12 ,,	Sporadic divisions occurring.
6.00 ,,	14 ,,	Cell outlines less distinct: still a Morula.
8.00 ,,	16 ,,	Cell divisions still occurring: cells less turgid.
10.00 ,,	18 ,,	Much the same.
12.00 noon	20 ,,	About 64 cells, Morula still.
3.00 p.m.	23 ,,	Much the same.

The slowness of the division is no doubt to be correlated also with the large amount of yolk. In the echinoderm Antedon petasus the embryo leaves the egg at about the twenty-fourth hour (Mortensen, 1920).

3. From the Morula to the late Blastula.

During the succeeding twenty-four hours cell-division continues; the boundaries between cells becoming less and less obvious in the living object. When viewed in strong sidelight under a dissecting microscope the slight elevations of the outer surfaces of cells are thrown into relief, and indicate that the embryo comprises some hundreds of cells, so pressed together as to produce a polygonal 'honeycomb' pattern on the exterior. When about two days old the embryo is spherical, with an almost smooth external surface. A vertical section shows that

a small irregular blastocoel is present in the central region, rather nearer the animal pole than to the vegetal one. It is occupied by a fluid apparently of some density, which coagulates in ordinary fixatives. It then readily stains with aniline blue, but does not take up fuchsin, methyl orange, or light green. When coagulated and unstained it has a pale straw-colour in sections of about 16 microns thickness. The cells comprising the wall of the blastula are two or three layers in thickness about the animal pole, and apparently more in the vegetal hemisphere (fig. 18, Pl. 21). As nuclear stains cannot be used the cells are difficult to demonstrate (see Technique, p. 387). The yolk granules are seen to be distributed with equal density in the animal and vegetal hemispheres, while the peripheral cells of both hemispheres are lighter in colour and less heavily yolked. The yolk-granules stain deeply with methyl orange, while the remaining cytoplasm takes up acid Fuchsin readily. When Heidenhain's haematoxylin is employed the blastocoel fluid becomes a deeper shade of straw-colour, and the yolk granules become intense black. Methyl green stains only the cytoplasm, between the granules. No cilia are developed.

4. Gastrulation.

About the beginning of the third day the formation of the gastrula commences and continues slowly throughout the succeeding two or three days.

The first indication of the beginning of this process is the gradual flattening, and then inpushing, of the vegetal pole (fig. 15, Pl. 20; figs. 19 and 20, Pl. 21). This involves first the reduction of the blastocoel to a small cavity, crescent-shaped in vertical section (fig. 19, Pl. 21), with its convex border directed towards the animal pole. The micromeres thus come to shape a dome, into the hollow of which the macromeres project as a solid cone of cells. In a rather older embryo a pronounced rim becomes obvious about this inwardly projecting mass, and on two sides the rim is more highly developed, and comes to form two crests which move toward a median position. When viewed from the exterior in a living embryo a curious resemblance to a zygote developing the furrow of its first cleavage is noted.

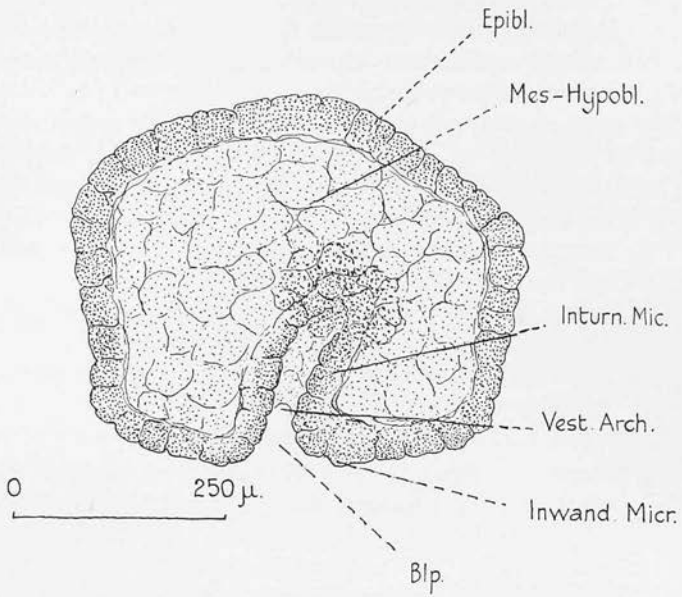
A study of sections through stages preserved at different times during this period indicates that a long process of epibolic inwandering of micromeres takes place, this latter process accounting for a very large proportion of the mes-hypoblast. This process was observed taking place in the living embryo. The more intensive inturning of the micromeres along two sides of the vegetal hemisphere produces the observed crests (figs. 16 and 17, Pl. 20; figs. 20, 21, and 22, Pl. 21). The fact that these should occur, indicating perhaps a tendency to bilateral symmetry, is extremely interesting, as being the sole vestige of this type of symmetry which is ever observable in the embryo.

Epiboly is not by any means confined to these crests, occurring all round the rim of the blastopore, and only to a more marked extent on the crests. Longitudinal sections through the median vertical plane of the embryo between the crests, and not cutting them, indicate this fact. When the crests are cut in transverse vertical section (figs. 20 and 21, Pl. 21), it is seen that they are growing over the mes-hypoblast already formed by invagination. When the plane of sectioning is parallel to the median vertical plane between the crests, but a little to one side, so as to cut the crest itself, the latter shows as a separated zone lying on the hypoblast (figs. 22 and 23, Pl. 21). The combined process of invagination and epiboly results in the steady reduction of the size of the blastocoel. It becomes pushed nearer to the animal hemisphere and assumes a very attenuated crescent form in vertical section, till its cavity is finally obliterated (fig. 23, Pl. 21). The epiblast now lies in contact with the hypoblast. As mentioned above, the fluid of the blastocoel when coagulated stains with aniline blue. Making use of this property it is possible to follow the subsequent movement of the zone formerly occupied by the blastocoel, as it remains distinguishable as a thin blue line between epiblast and hypoblast.

The small opening around which are the cells of the epiblast crests obviously represents the blastopore, but of the archenteron nothing but a vestige is produced. The transient space occupied by loose cells just within the blastopore is all that can be spoken of as the 'archenteron' (fig. 23, Pl. 21, and Text-fig. 1).

The small invagination which occurs takes place early in

gastrulation during the third day. During subsequent days epiboly continues, affecting only the outer layer of micromeres, which thus becomes considerably reduced in thickness owing to the large contribution it makes to the hypoblast. In the region



TEXT-FIG. 1.

Late gastrula, vertical section showing the epiboly in its later stages. *Epibl.*, epiblast; *Mes-Hypobl.*, mes-hypoblast; *Inturn. Mic.*, inturned micromeres; *Vest. Arch.*, vestigial archenteron; *Inwand. Micr.*, inwandering micromeres; *Blp.*, blastopore.

of the blastopore the inturning layer can be readily seen in suitably stained preparations, and traced a considerable distance into the central mass of hypoblast (see Text-fig. 1). During all the latter portion of the epibolic process the crests are not observable, being transient features associated with the early part of gastrulation. I have not been able to relate the median plane of this earlier stage with any structure or plane of symmetry of the adult, owing to the later movements of the embryo within the egg membrane. It is, however, quite clear that the

blastopore occupies the position of the future mouth, the face of the embryo opposite to it thus being dorsal (aboral). Thus, as early as the third cleavage the future regions of the animal are broadly indicated, the micromeres being dorsal (aboral), and the macromeres ventral (oral). As the process of fertilization has not been observed, it cannot be stated whether these regions are determined at that time, though from analogy with other cases this would seem probable.

The state of the embryo at this stage may be summarized here:

(1) Epiblast, derived from part of the micromeres, overlies.
(2) Mes-hypoblast, derived from invaginated macromeres and epiboly of micromeres.
(3) The blastocoel is obliterated.
(4) The archenteron is a bare vestigial depression in the hypoblast.
(5) The blastopore occupies the position of the mouth, and thus is ventral.
(6) No indications of the future lines of symmetry are visible.

The process of gastrulation is further discussed on p. 433. It will be seen to bear no relation to the process of 'delamination' described by Russo in Amphiura squamata, and stated by him to be responsible for the formation of epiblast and hypoblast. Rather it is to be compared with the process followed in the Frog, with the reduction of the archenteron carried to a much greater extent.

5. The Assumption of Radial Symmetry.

At about the sixth or seventh day there are indications that the embryo is assuming a radially symmetrical form. This is first made evident by the appearance of five grooves running outward from the blastopore region on the ventral side of the embryo (figs. 24 and 25, Pl. 21). At the same time a gradual flattening of the embryo begins, this affecting the ventral aspect first. The embryo is still without any internal cavities; the archenteron has quite disappeared, and the position of the blastopore is visible externally as a central depression on the ventral side. By about the tenth day the embryo has assumed

the form of a somewhat flattened hemisphere, slightly indented at five equally spaced points round its periphery, corresponding with the tips of the five grooves. Its ventral surface is now almost flat, while the dorsal surface is in the form of a low dome. On the ventral surface, near the periphery, ten equally spaced rounded projections are developing (figs. 26 and 27, Pl. 21). These at first have a superficial resemblance to macromeres projecting from the vegetal pole of a blastula. These ten lobes are the rudiments of the podia. At the centre of the ventral surface, in the former blastopore region, the depression is deeper, and continues to deepen in the succeeding development. This hollowing out is the forerunner of the cavity of the definitive enteron.

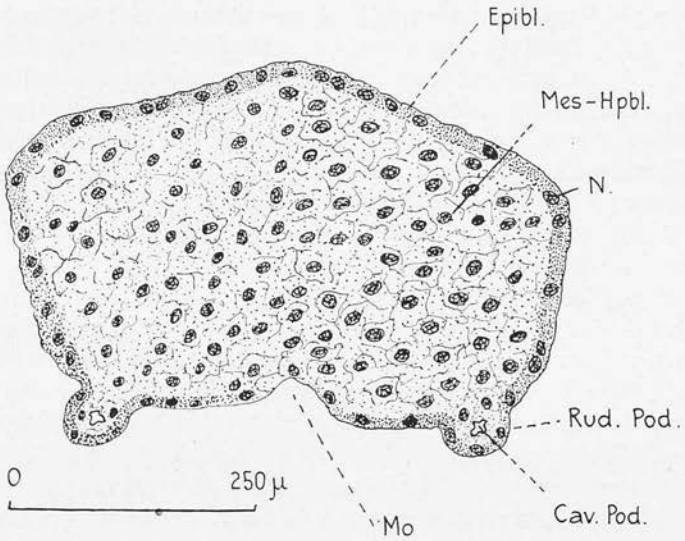
Owing to its characteristic appearance this stage can be conveniently referred to as the 'Rosette'.

In vertical section the rosette stage shows a large, solid, central zone of mes-hypoblast, its cells small, and densely laden with yolk granules. This is surrounded by a narrow zone of epiblast cells, staining more darkly with cytoplasmic dyes, owing to the smaller proportion of yolk present in this region. On the flattened ventral surface the depression is seen in the blastopore region as a simple cone-shaped excavation penetrating the ventral-most zone of mes-hypoblast. The podia on either side of the mouth region show as solid projections, apparently containing both epiblast and mes-hypoblast, and with a faint lighter zone in the centre of each, this being the first indication of the process of splitting which shortly afterwards occurs at that point (Text-fig. 2).

6. Origin of the Hydrocoel.

During the succeeding three days after the appearance of the rudiments of the podia all developmental changes are clearly in the direction of the definitive adult form. The disc flattens still more till it assumes a lens shape of approximately equal curvature on dorsal and ventral surfaces. Meantime the podia lengthen, and group themselves into five pairs. The subsequent development shows that the five grooves of the rosette stage are in no way related to the ambulacral grooves of Asteroidea, being

merely the interradial depressions between the more bulging radii. While the podia are thus altering externally, sections reveal that an important internal change is taking place. In each podium a splitting occurs in the central zone, which was derived from mes-hypoblast. The result of this splitting is at

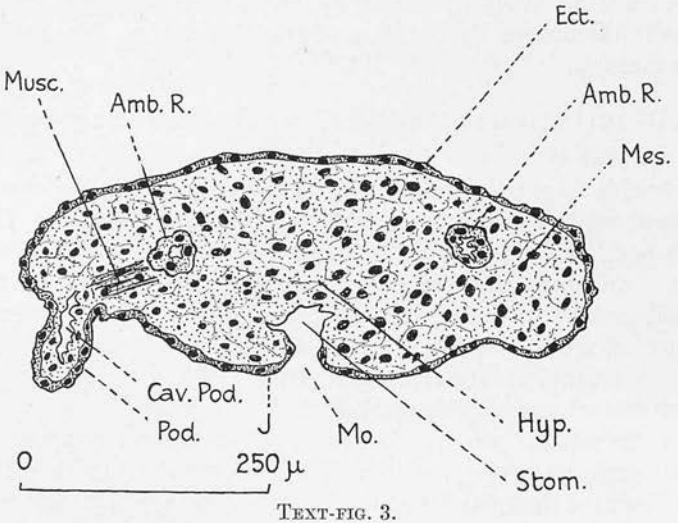


TEXT-FIG. 2.

Rosette stage, vertical section showing origin of the podia and mouth. *Epibl.*, epiblast; *Mes-Hypobl.*, mes-hypoblast; *N.*, nucleus; *Rud. Pod.*, rudiment of podium; *Cav. Pod.*, developing cavity in podium; *Mo.*, rudiment of mouth.

first an irregular cavity with its lining cells projecting into it (Text-fig. 3), but later it becomes smoother inside. Corresponding to the splitting in each podium, in the central mes-hypoblast, about half-way between the podia and the centre, the ambulacral ring is similarly developing as a circular split surrounding the future enteric region. The podial cavities achieve a connexion with the ring canal, apparently by continuation of the splitting process, and the functional hydrocoel is thus brought into being. Of the origin of the madreporic canal I have been unable to

obtain clear information. In some specimens there is an irregular series of fine splits running from the ambulacral ring to the dorsal surface of the embryo, and it seems probable that these are in some way related to the definitive madreporic canal. The spongy character of the tissues at this stage would probably permit readily any direct absorption of water through them under protoplasmic activity. Corresponding to the development of the hydrocoel, the cavity of the gut is also inpushing steadily



TEXT-FIG. 3.

Disc stage, after emergence from egg, vertical section. *Ect.*, ectoderm; *Amb. R.*, ambulacral ring; *Mes.*, mesoblast; *Hyp.*, hypoblast; *Stom.*, stomach; *Mo.*, mouth; *J.*, jaw; *Cav. Pod.*, cavity of podium developing by splitting; *Pod.*, podium; *Musc.*, muscle-fibres of podium.

in the form of a broad split in the lower and central zone of the hypoblast (Text-fig. 3).

At about the fourteenth day the embryo makes its first movements. A slow, feeble extension and contraction of the podia is observable occasionally.

7. Birth of the Embryo.

During the twenty-four hours which succeed the first signs of

movement the embryo becomes more and more active. The podia are worked up and down steadily, pressing against the egg-membrane and stretching it. There appears to be no co-ordination between the movements of the podia, each podium moving independently and out of step with its fellows. At the same time the embryo moves round within the egg-membrane, so that all the latter receives its share of the stamping process and becomes thrown into wrinkles. At length the membrane breaks horizontally by several splits, and the young ophiuroid slowly disengages itself and emerges, to begin at once active progression.

8. Description and Behaviour of the Young Ophiuroid.

At this stage the young animal presents a rounded pentagonal disc about 0·05 cm. in diameter and 0·015 cm. in thickness. The ten podia are arranged near the periphery of the lower surface about 0·006 cm. from the margin, a pair to each of the arm buds. Each podium when fully extended reaches about 0·017 cm. from the disc, and is bent downwards at a position just below its point of separation from the disc (fig. 29, Pl. 21). The podia are almost transparent, and slightly clubbed at the extremity. They do not bear 'bristle-like processes'. Each is subtended on its upper and outer side by a very small papilla-like structure, which is the rudiment of the spine borne by the future adoral plate. The oral aperture is at this stage small.

The young animals are quite active and move about continuously, though if the container receive a slight knock they temporarily retract their podia and remain motionless. Their manner of progression is characteristic, and appears very awkward. The podia are held rigidly so that the animal is perched on ten vertical pegs. Movement is achieved by stiffly swinging the podia from the points at which they are bent downward. They appear to wander about in a manner which could best be described as 'entirely aimless' if it were proper to apply such terms to Echinoderms! They take no food, evidently still obtaining nourishment from the yolk in the tissues.

Strong light appears to have a narcotic effect, and movement

is suspended. If subjection to strong light is continued, death follows. In the aquarium tank most individuals are to be found beneath stones, but many are uncovered. Chloral hydrate in dilute form has a gentle narcotic effect, but ether produces violent contraction and distortion (see Technique, p. 386).

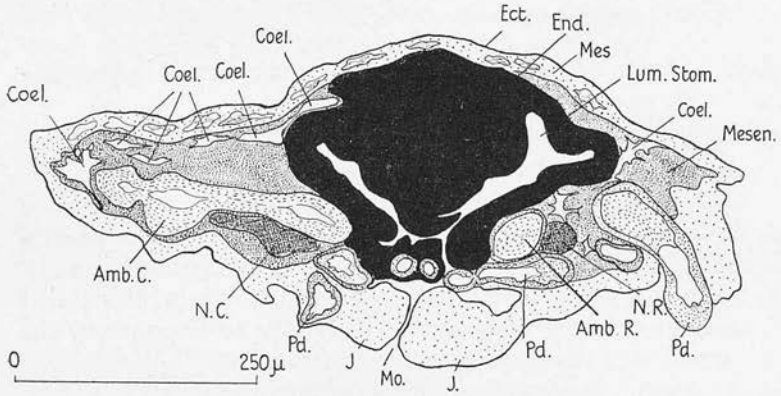
When five days old the free living form presents roughly the outline of the starfish Asterina. The arms can be turned dorsally and ventrally, but not from side to side. The jaw regions are distinguishable.

9. Origin of the General Coelom: Associated Internal Differentiation.

Up to the present (i.e. about nineteen or twenty days from the first cleavage) the only cavities present in the animal are (*a*) the developing enteron, (*b*) the hydrocoel. For the first five days or so after emergence from the egg the remarkable condition obtains of a freely active young ophiuroid without a general body cavity. But during this period internal changes are occurring which are to bring about the formation of the main coelomic cavity.

A vertical section through an ophiuroid of about five days' free life shows the following differences in internal structure from the condition before leaving the egg: the mes-hypoblast is distinguishable as a thick central mass of tissue in which the yolk is concentrated. The yolk has disappeared from the outermost tissues. The cavity of the gut has extended upward through the mes-hypoblast mass so as to assume the form of a hollow cone, at the apex of which is the mouth; into the base of the cone, on the upper side, the remaining mass of mes-hypoblast hangs as a rather smaller solid cone (Text-fig. 4). Surrounding the gut, and evidently derived from its outer layers, is a zone of spongy cells containing yolk-granules, and staining more lightly with acid Fuchsin than the gut itself. This mass of tissue may be termed mesenchyme by analogy with corresponding tissues in the embryos of other animals. Its cells, though loose, are not provided with processes enclosing spaces, as is the case in typical mesenchyme. On the inner (oral) side, about the region of the future oesophagus, a small set of buccal

tentacles is developed from the ring canal. At the time when the hydrocoel originally appeared, the tissue in which it formed could not be distinguished from the central mes-hypoblast mass. The podia themselves, at their earliest stage, are comprised of yolk-laden cells, but the yolk disappears by the fifth day. In the outer regions of the body a spongy light-staining zone indicates the mesoderm evidently derived from the outermost



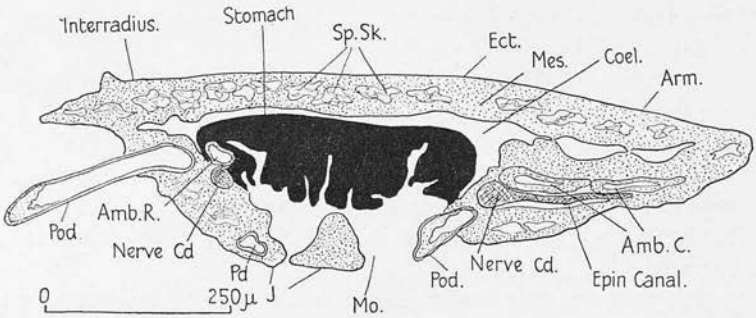
TEXT-FIG. 4.

'Asterina' stage, vertical section (partly diagrammatic), showing origin of coelom by splitting. *Ect.*, ectoderm; *End.*, endoderm; *Mes.*, outer mesoderm; *Lum. Stom.*, lumen of stomach; *Coel.*, coelomic splits *Mesen.*, mesenchyme; *Pd.*, podium; *N. R.*, nerve ring; *Amb. R.*, ambulacral ring; *J.*, jaw; *N. C.*, nerve cord; *Amb. C.*, ambulacral canal.

layer of the mes-hypoblast. It is of a very spongy, mesenchymatous texture, but, unlike the tissue between it and the gut, it retains this form throughout all the stages subsequent to this that have been studied by me. On the other hand, the tissue between it and the gut, which is here called 'mesenchyme', soon changes its structure, and becomes entirely altered between the fifth and the tenth days. On either side of the gut, and in the arms, small cavities develop between the component cells of the mesenchyme. These extend and unite to form the general body cavity. The last region to be affected is dorsal to the gut.

By this process the gut becomes separated from the body-wall by a single cavity lined by a thin layer of the mesenchyme cells. The process is complete by the tenth day of post-embryonic life. At the same time the ambulacral system becomes underlaid by narrow splits, also in the mesenchyme tissue, resulting in the formation of the perihaemal cavity (see Text-figs. 4 and 5).

Below the ambulacral canals and oral ring are seen the nerve cord and ring. Their origin I have not been able satisfactorily



TEXT-FIG. 5.

Stage after completion of the general coelom, vertical section, cutting arm on right, and interradius on left, partly diagrammatic. *Sp. Sk.*, spaces left after solution of calcareous skeletal plates; *Ect.*, ectoderm; *Mes.*, mesoderm; *Coel.*, general coelom; *Amb. R.*, ambulacral ring; *Amb. C.*, ambulacral canal; *Epin. Canal.*, epineural canal; *Nerve Cd.*, nerve cord; *Pd.* or *Pod.*, podium; *Mo.*, mouth; *J.*, jaw.

to determine, but it would seem to be almost certainly from the ectoderm of the ventral surface.

The foregoing stages of development are discussed below, after the treatment of the skeletal system.

It is seen that what has been referred to as 'mes-hypoblast' in this account comprises both the future mesoderm and the endoderm, though these components are not distinguishable structurally till the fifth day or so. Obviously the mesoblast and true hypoblast must be differentiated earlier than the time when they become visibly distinguishable. The true mesoblast tissue includes that in which the hydrocoel is excavated. The true

hypoblast comprises only that tissue which is to form the definitive endodermal lining of the stomach.

Thus, although the coelom is not derived from archenteric pouches, the mesoderm in which it finally develops by splitting is itself derived originally from the mes-hypoblast of the archenteric wall.

VII. Later Development.

The later development of the young ophiuroid, so far as it has been followed, results only in the fuller expression of the organs so far described.

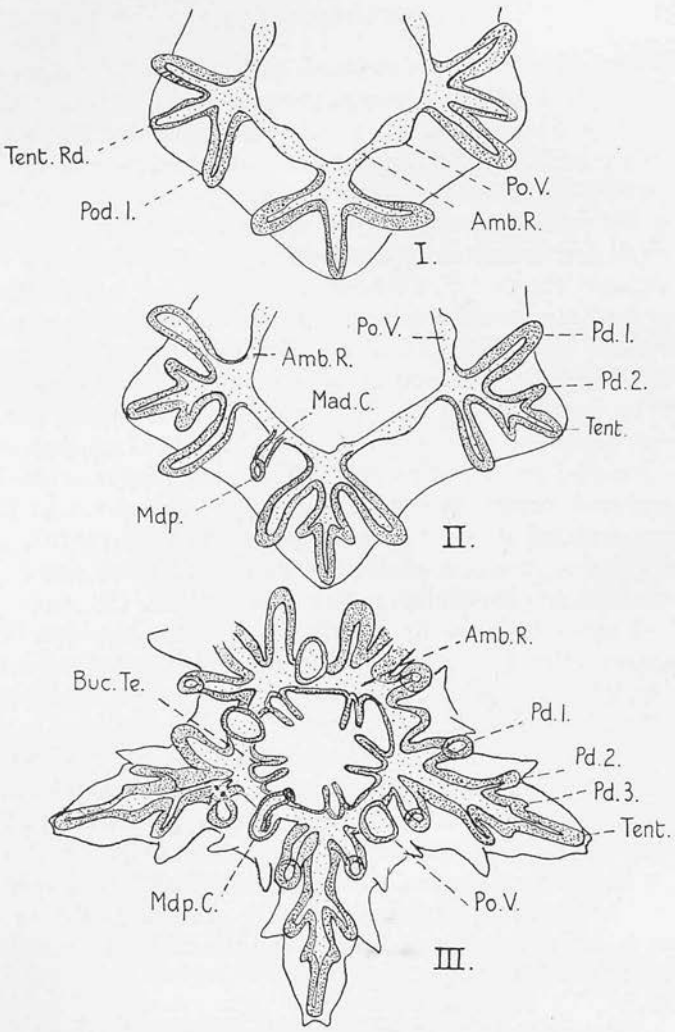
At about the fifteenth day of post-embryonic life the arms are showing the first definite signs of segmentation (fig. 32, Pl. 21). The first segment begins to be demarcated from the terminal region. With the later growth of the arm the terminal region is carried outward practically unchanged, and new segments are added just behind it, and in front of the youngest segment.

The yolk granules finally disappear from all parts of the body except the gut wall. The animal then has the appearance of a pale, transparent, rose-coloured star with a central zone (the stomach) showing a deep terra-cotta. The nutritive matter of the gut is gradually used up, this process being accompanied by the excavation of the gut wall by numerous cavities. These extend till the spaces between them are mere folds of endoderm epithelium forming a honeycomb pattern on the gut wall.

At the apex of the arm the ambulacral system extends by outward growth. The rudiments of the podia of the next segment to form are visible within before the segment is itself externally differentiated. The extreme aboral ends of the ambulacral canals function as small tentacles protruding through the neural groove in the terminal plate. Stages in the development of this system are shown in Text-fig. 6.

The skeleton begins to form at the stage intermediate to that with two arm-segments and that with three, and thus is considerably delayed. Its development is treated separately in a subsequent section of this paper.

The muscular system differentiates first in the walls of



TEXT-FIG. 6.

I., ambulacral system of newly hatched ophiuroid. Reconstructed from vertical and horizontal sections. II., ambulacral system of 'Asterina' stage. III., ambulacral system of stage having two arm-segments. *Po. V.*, polian vesicle; *Amb. R.*, ambulacral ring; *Pd.* or *Pod. 1, 2, 3*, first, second, and third podia; *Tent. Rd.*, rudiment of tentacle; *Mdp. C.*, madreporic canal; *Mdp.*, madreporite; *Buc. Te.*, buccal tentacle.

the first set of podia, developed while still within the egg-membrane. The fibres are most strongly developed at the base of each podium, and give it a striated appearance. The fibres take up acid Fuchsin strongly—also carmine. The region of hypoblast in the rosette stage in which the hydrocoel first appears evidently represents a mesodermal region of endodermal derivation, and it is this which gives origin to the muscles of the body, and later of the arms, as they develop. The first arm muscles to form are the dorsals and ventrals. These are differentiated and functional (so far as the unsegmented condition permits) as early as the fifth day of free life. By the eighteenth day the jaws are capable of distinct movement, though no food is taken in. At about the twentieth day the arms are longer and capable of lateral movements, while the dorsal and ventral muscles are strongly developed. At this stage, and for all succeeding stages observed (i.e. up to the formation of seven arm-segments), a curious muscular reaction to mechanical stimuli such as shocks is observed. The arms are folded upwards on to the dorsal surface of the disc—recalling the conventional diagram showing the derivation of the echinoids from asteroids. As the arms grow longer, when this position is assumed the arms cross; and still later are coiled about each other, to give the whole animal a spherical form, which rolls about freely when knocked and appears quite lifeless. This obviously is a protective adaptation similar to the spider, which 'feigns' to be a piece of earth or twig.

By the stage of five or six arm-segments the animal has used up nearly all the yolk and begins to take in food. In the aquarium tank used, masses of diatoms and other minute algae were taken in for this purpose.

VIII. The Development of the Skeletal System.

A. Introductory Remarks.

The literature dealing with the skeletal structures of Ophiuroids, more especially that dealing with the developmental aspect, suffers from an unfortunate reduplication and confusion of terminology. This has arisen partly from the bestowal of a multiplicity of terms by various independent workers on the

same structure, and partly through the application by different authors of the same name to entirely different structures. To avoid adding further to the confusion I append below a list of the terms used by me for the skeletal plates which have come into this study, together with such synonyms as are used in the literature available to me. In general I have selected the terms at present in use by such modern systematists as H. L. Clark, R. Koehler, and Th. Mortensen. In certain cases, however, it has been necessary to use other terms to avoid confusion.

Unrecorded Structures.—While reluctant to add to the existing mass of names employed for skeletal structures in Ophiuroids, for the sake of rendering my descriptions intelligible, I am forced to give names to certain definite structures of regular occurrence, but not described or referred to in the literature available to me. The detection of these structures I owe to the use of polarized light.

In at least one case the use of polarized light and photography has cleared up a point previously in dispute. I refer to the development of the torus angularis and the tooth.

Points of interest are discussed as they arise.

B. Nomenclature adopted.

1. Plates of the Calyx.

Centro-dorsal.—That single pentagonal plate occupying the centre of the primary calycinal system of plates (Text-fig. 7, *C-D*). Clark (1911), Ludwig (1882), Delage and Hérouard (1903), Koehler (1907).

Synonyms.—(*a*) Dorso-central. Fewkes (1887), Russo (1891), (*b*) Centrale. (Quoted by Delage and Hérouard.)

Radials.—The five radially situated plates which form about the centro-dorsal, and which retain this position (Text-fig. 7, *Rd.*). Fewkes (1887), MacBride (1914).

Synonyms.—(*a*) Deuxièmes radiales primaires, Delage and Hérouard (1903), (*b*) Radialia, (*c*) Basals, A. Agassiz, and others.

Note: These plates are often confused with the terminal plates (q.v.). They differ from the latter in that they do not migrate outward when the arms begin to develop. They have no connexion with the 'Radial Shields' of adult Amphiuridae.

Oral Shields.—The five interradial plates which form between and outside the Radials, and later migrate to the ventral surface of the disc to contribute to the oral skeleton (Pl. 22, *Or. S.*). Matsumoto (1915), Clark (1911), Mortensen (1920).

Synonyms.—(*a*) Pièces orales, Delage and Hérouard (1903), (*b*) Boucliers buccaux, Koehler (1907), (*c*) Mouth shields, Hutton (1872), Koehler (1907), (*d*) Buccal shields, Bather (1901).

Note: Not to be confused with the Oral Plates (q.v.).

2. Plates of the Arm.

Terminal.—The unpaired plate which forms in the apical segment of each arm, and is carried outward in the growth of the arm in length (Text-fig. 7, *T.*). Fewkes (1887), Ludwig (1882), Delage and Hérouard (1903), Mortensen (1924).

Synonyms.—(*a*) Erste Anlage der Wirbelstücke (a mistaken identification), Metschnikoff (1869), (*b*) Premières radiales primaires (also an incorrect name), Delage and Hérouard (1903), (*c*) Erste Anlage der Arme, Max Schultze (1852).

Note: Confused by some writers with the ambulacrals, also with radials.

Dorsal (Brachial) Plates.—The unpaired series of radially situated plates which form in centrifugal order on the dorsal surface of the arm, between the radial and terminal plates. Koehler (1907), Clark (1911), Mortensen (1924), and others.

Synonyms.—(*a*) Radiales secondaires, Delage and Hérouard (1903), (*b*) Rückenschilder, (*c*) Scutella dorsalia, also 'Upper arm-plates', 'Upper ray-plates' (Hutton), 'Dorsal arm-plates', 'Dorsales des bras', &c.

Ventral (Brachial) Plates.—Corresponding to the dorsals, but on the ventral surface, between the peristomial plates (q.v.) and the terminal (Pl. 22, *V.*). Koehler (1907), Clark (1911), Mortensen (1924).

Synonyms.—(*a*) Épineurales, Delage and Hérouard (1903), (*b*) Sous-ambulacraires, Ludwig (1882), (*c*) Bauchschilder, (*d*) Scutella ventralia, (*e*) Super-ambulacralschilder, J. Müller; also 'Lower ray-plates' (Hutton), 'Under-arm-plates', 'Ventral arm-plates' (Fewkes), &c.

Lateral (Brachial) Plates (= adambulacrals).—The paired series of adambulacral plates forming in centrifugal order along the sides of the arms, between the dorsal and ventral brachial plates. They bear spines (Pl., 22, *L.*). Koehler (1907), Clark (1911), Mortensen (1924).

Synonyms.—(*a*) Lateral arm-plates, A. Matsumoto (1915), Fewkes (1887), (*b*) Laterals, (*c*) Adambulacraires, (*d*) Seitenschilder, (*e*) Scutella lateralia, also 'Side arm-plates', 'Side ray-plates', &c.

Vertebrae (= ambulacrals).—The endoskeletal radially situated ossicles forming in centrifugal order within the arm (Text-fig. 10). This term now in general use.

Synonyms.—(*a*) Ossicules discoides, (*b*) Plaques ambulacraires, (*c*) Vertebral ossicles, Bather (1901).

3. Plates of the Oral Skeleton.

Oral Shields.—(Vide 1. Plates of the Calyx.)

Adoral Plates.—The paired interradial plates regarded as the second pair of the adambulacral series, forming to the sides of, and adorally to, the oral shields, and aborally to the plates which fuse to form the oral plate (q.v.) (Pl. 22, *Ad. 2*). In the young form each bears a single spine. Clark (1911), Koehler (1907), Mortensen (1924).

Synonyms.—(*a*) Side mouth-shields, Bather, and many others, (*b*) Seitenmundschilder, (*c*) Scutella adoralia, (*d*) Adoral shields, Matsumoto (1915).

Oral Plates.—The structures supporting the torus angularis and teeth (q.v.) on their adoral side, and forming interradially on the adoral sides of the adoral plates. Each oral plate arises in development from the fusion, or close appression, of two 'Semi-angular plates', each of these latter being derived from the interradius. Each semi-angular plate is in turn derived from the fusion of an ambulacral and an adambulacral plate of the same side. This complex structure will be considered in more detail later (Pl. 22, *S. Ang.*). Clark (1911), Koehler (1907).

Synonyms.—(*a*) Jaws—of many authors (but not the 'Jaws' of Bather (1901)), (*b*) Pièces angulaires, Delage and Hérouard (1903), (*c*) Oral angle-piece, McMurrich (1906), (*d*)

Scutella oralia, (*e*) Ossa angularia oris, (*f*) Mâchoires, (*g*) Mundeckstücke, (*h*) 'V-shaped Plates' (of Apostolides).

Note: The term 'semi-angular' used above is equivalent to the 'syngnath' of Bather (1901).

Torus angularis.—The transverse plate formed at the apex of the oral plates and supporting the teeth (Pl. 22, *To.*).

Stated (incorrectly) by McMurrich to be derived from the teeth! This term in general use.

Synonym.—(*a*) Jaw-plate, Bather (1901).

Teeth.—The spine-like structures formed one by one on the adoral surface of the torus angularis (Pl. 22, *T.*).

Fewkes (1887) thought it probable that the teeth were derived by outward growth of the torus angularis. As will be shown in this paper, the teeth are each derived from the fusion of a number of independent paired interradial structures of definite number and relationship. Its connexion with the torus angularis is only secondary.

Synonym.—Palae angulares, McMurrich (1906).

Peristomial Plates.—The paired radial structures forming between the oral plates and eventually assuming an interradial position on the dorsal faces of the latter. Regarded variously as ambulacrals or superficial additions (Pl. 22, *P.P.*). MacBride (1906), Delage and Hérouard (1903), Matsumoto (1915).

Synonyms.—(*a*) First Ambulacrals, Ludwig (1882), (*b*) Spoon-shaped plates, Fewkes (1887).

The following two terms I have dropped altogether:

'Mouthframe'.—By Bather (1901) used synonymously with Ludwig's 'Second ambulacral' (which Fewkes suggests may indeed be a 'First ambulacral').

By MacBride (1906) used apparently as an inclusive term for the ring of modified arm-ossicles contributing to the oral skeleton.

The term 'oral frame' has been used by Matsumoto (1915) but it is not clear to me to what structure he applied it.

'Jaw'.—Employed variously for (*a*) The oral plate of Koehler, Clark, and others, (*b*) The 'first adambulacral' of Ludwig, by Bather.

In any case, as MacBride (1906) points out, there is no

evidence to show that this structure has a masticatory function.

C. Observations by Polarized Light.

As already mentioned in the section on Technique, the calcareous plates are, in their earliest stages, extremely difficult to observe owing to their minuteness and transparency. Accordingly, the method described on p. 389 is of great value for these early stages. As I am not aware of literature referring to this method, a few general observations will not be irrelevant here.

The calcite plates formed organically in the outer mesoderm of the body of the Ophiuroid show the following characters, typical for the most part of the mineral in its inorganic occurrence. Each plate is anisotropic—showing up with a brilliant golden light under crossed nicols, the remainder of the tissues being darkened. Owing to the high birefringence of the mineral, the plates frequently show bright green, red, and blue tints, this effect being enhanced as growth in thickness proceeds. I have never observed twinning to occur in the organic state. Extinction takes place on two axes at right angles to each other; a plate thus extinguishes four times at regular intervals of 90° when rotated on the stage. This effect must be taken into account when observing a stationary preparation, as otherwise any extinguished plates are liable to be overlooked. In the case of structures such as the peristomial plates (the 'spoon-shaped' plates of Fewkes), the length of which considerably exceeds the breadth, I find that the longer and shorter axes of the plate roughly correspond with the extinction axes of the crystal composing the plate. This observation is most interesting as indicating that a definite relation must exist between the orientation of the calcite molecules and the shape and position of the skeletal plate in which they occur.

When observing the extinction angle, care must be taken that two plates do not overlap—for an interference thereby results which frequently has the effect of preventing any extinction whatever.

In the case of a plate such as the tooth (q.v.), which arises

from the fusion of a number of parallel independent spicules, all the spicules extinguish at the same time, even while each spicule is still isolated from its neighbours. This remarkable 'foresight' as it were of the protoplasm of this region would seem to indicate that the whole process of spicule secretion is under some central co-ordinating influence—perhaps nervous, perhaps chemical. The writer suggests that hormones may be responsible. Further study of this interesting feature might yield useful information.

A further use for the extinction properties of calcite was found in determining the boundary between the two plates which fuse to form the semi-angular—for one element can be examined and photographed independently while the other component remains extinguished and invisible; whereas in ordinary light the plate shows no division externally, and appears of uniform structure. As will be further mentioned later, it was found that the crystalline axes of the two elements comprising this compound plate lie at an angle which is constant within certain limits. This latter result, when considered in the light of the former observations, would suggest that it is reasonable to suppose that in any plate of the Ophiuroid there exists some definite relationship between its gross morphology and its minute molecular structure.

This relationship must be capable of formulation.

D. Larval Skeleton.

No trace of a larval skeleton has been observed by me. This fact is, of course, to be expected in view of the complete suppression of any larval stage. In failing to develop any larval skeleton this species evidently resembles Ophiura brevispina, the development of which, described by Grave, is quoted by MacBride (1914). Ophiura, however, has a rather reduced non-pelagic, 'worm-like larva'. Amphiura squamata, on the other hand, with a very reduced larva which is never free-living, develops a provisional larval skeleton, as first pointed out by Max Schultze (1852) and figured by J. W. Fewkes (1887) and others.

E. Commencement of Skeletal Formation.

No skeleton is present till the stage of two arm-segments, when the rudiments of the radials, centro-dorsal, oral shields, and semi-angulars appear almost simultaneously.

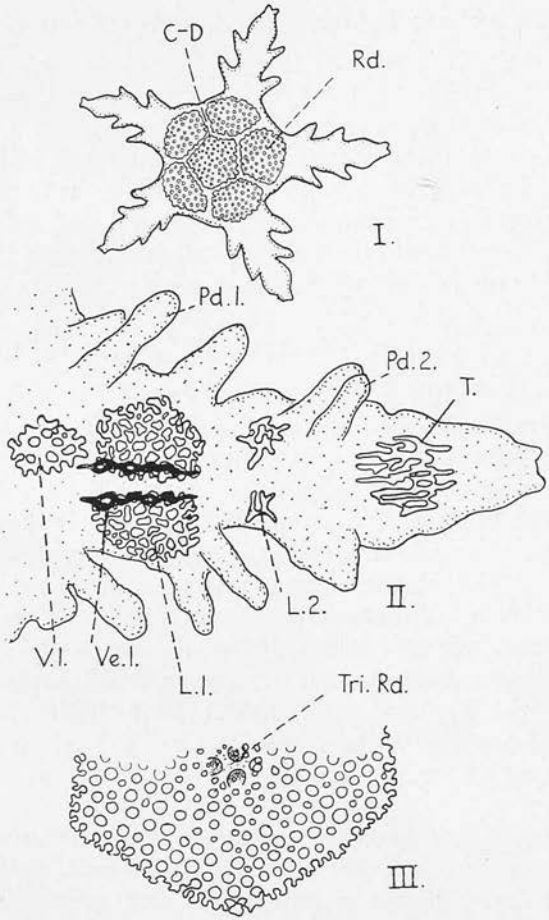
Skeletal formation is thus considerably delayed, for the young animal has been free-living for two to three weeks previously. In Amphiura squamata the rudiments of all the chief skeletal structures of the body are well defined while the animal is still in the pentagonal disc stage, within the bursa.

F. The Development of the Skeleton.

1. The Plates of the Calyx.

(*a*) Radials and Centro-dorsal.—The earliest stages of the development of these plates have not been observed by me. It seems that skeletal formation is delayed for a considerable period, and then occurs very suddenly and rapidly at some stage during the transition from the stage of two-arm segments to that of three. This phenomenon is consistent with the suggestion above that spicule formation is controlled by the liberation of a hormone. The point will be further discussed at the conclusion of this paper. In the accounts of Agassiz (1877), Ludwig (1882), Delage and Hérouard (1903), and A. Russo (1891) it is agreed that the first rudiments of each of these plates is a triradiate spicule, and it seems reasonable to assume that this is the case here.

In the earliest specimen I have observed, a centro-dorsal is surrounded by a ring of rather larger pentagonal radials. The smaller size of the centro-dorsal would seem to indicate that it has a slightly later origin than the five radials, but I am not certain on this point. In the case of Amphiura squamata Agassiz (1877) states: 'We have the most positive proof of the origin of the dorso-central plate of Starfishes and Ophiurians . . . simultaneously with the five basals.' But Ludwig (1882) contradicts this, saying, 'Diese sechste Platte, das Centrale tritt bei Amphiura squamata in der Regel später auf als die fünf Radialia.' Fewkes (1887) considered that Ludwig was right in this respect, but evidently was not certain on the point. I regret



TEXT-FIG. 7.

I., calycinal system, except oral shields. II., arm-plates at stage of I. III., portion of radial plate. *C-D*, centro-dorsal; *Rd.*, radial; *T.*, terminal; *Pd. 1, 2*, first, second podia; *L. 1, 2*, first, second laterals; *V. 1*, first ventral; *Ve. 1*, first vertebral rudiments; *Tri. Rd.*, triradiate rudiment.

that I have not been able to contribute definite information as a result of my own observation.

In the earliest form in which I have observed them these

plates present symmetrically placed pentagonal outlines, separate each from the other by a narrow interval. As development proceeds this interval disappears, and the plates eventually overlap one another at their edges. Each plate consists of a perforated calcareous expansion, indented at the edge (where increase in size is occurring). The perforations near the centre are smaller than those near the edge, and in older plates the central perforations appear almost obliterated. Near the central zone of some of the plates a small triradiate ridge is observable, and it seems possible that this may be related to the original triradiate spicule from which the plate is supposed to have been formed. I have drawn this structure in Text-fig. 7, III.

(*b*) Oral Shields.—These arise interradially in a similar manner to that described for Amphiura squamata. However, they earlier reach a greater size than the surrounding ossicles, unlike Amphiura as figured by Fewkes. When first observed these plates were already on the edge of the disc, the ventral apex of each being directed adorally between the developing semiangulars. One of these plates is destined to become a madreporite, but even in the oldest specimens reared by me no sign of differentiation of any of the oral shields is observable. The adoral edge of each oral shield is slightly overlaid by the aboral edges of the developing second adambulacrals (destined to become adoral plates on either side of the oral shield).

2. The Plates of the Arm.

(*a*) The Terminal Plate.—In regard to the development of the terminal plate the literature is confusing. Before recording my observations on the matter it will be useful to summarize the present position.

Balfour (1881) stated: 'The original five radial plates remain as terminal segments of the adult rays.'

Ludwig (1882) showed that the terminals originate independently of the radials. The latter remain in the centre of the disc and are certainly not carried out into the arm. He was inclined to think that the terminals arose earlier than the radials. He used Amphiura squamata as his material.

Fewkes (1887) reiterates Ludwig's conclusion in regard to the independent origin of the terminals, but contradicts Ludwig's statement that the terminals precede the radials in appearance, saying, 'The terminals originate after the primary radials'.

Delage and Hérouard (1903) adopt on different pages of the same book the two opposing views as if they were compatible. On p. 112 it is stated: '. . . la première radiale primaire . . . est la terminale entrainée au bout du bras, et la deuxième radiale primaire . . . est la radiale définitive du pole apical'—thus adopting the old view of Balfour. But on p. 143 the same authors state: '. . . d'abord (apparaissent) les cinq radiales, puis, à peu près en même temps, la centrale et les cinq terminales.' thereby adopting Fewkes's statement.

MacBride (1914) adopted Fewkes's view. Accordingly I paid special attention to this point in the present species. I can say definitely that in this animal the terminal plates appear a f t e r and i n d e p e n d e n t l y of the primary radials, see Text-fig. 7. As skeletal formation is delayed in this species, the terminal plate is never at any time situated on the disc (as is the case in A m p h i u r a s q u a m a t a), but is always at the apical segment of the arm. Further, the five terminals do not all necessarily appear simultaneously, some being clearly differentiated while others are in the most rudimentary condition.

A further point on which a difference of opinion is expressed in the literature is as follows: Fewkes (1887) quotes Sladen (1884) as saying, 'The primitive structure and mode of formation of the terminal plate is different from that of the first radial'. On this statement Fewkes comments: 'It seems to me that the difference in primitive structure, if any, ought to have been more fully pointed out, and it is doubted whether there is any great difference in these particulars. I find nothing in Ludwig's account to justify the above statement of Sladen, and my own observations show that both the terminal plate and the first radial have many points of resemblance in "primitive structure" and "mode of formation". It is not intended to be denied that the form of the terminals and first radials may differ from the very first, or that they cannot be distinguished one from the

other.' Fewkes's figures show that he did not perceive any structural difference between the two plates concerned.

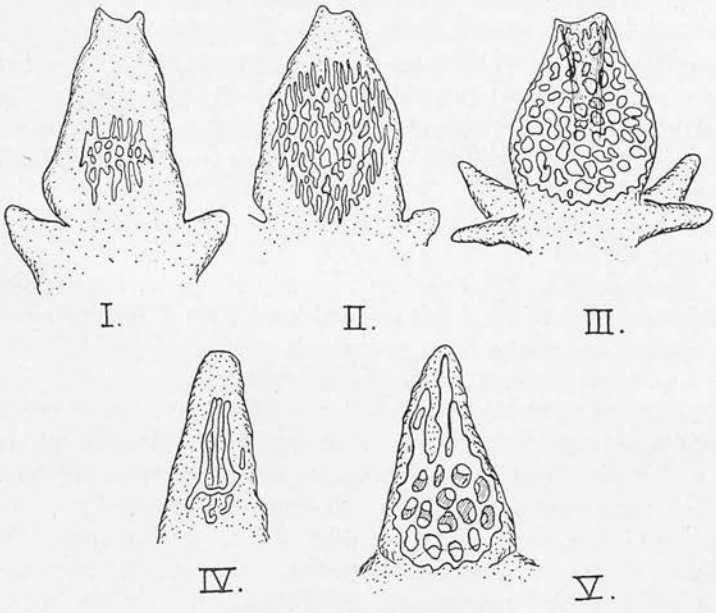
The present writer was struck by the marked difference between the growth of the terminal plate and all the other plates, including the radials. This is in contradiction to the views of Fewkes and Ludwig.

Whereas the other plates form plane expansions of calcite, perforated by approximately circular holes, the terminals are notable right from their earliest appearance for the attenuated nature of the calcareous matter and the elongate form of the perforations. To bring out this feature I figure three camera lucida drawings of stages in the development of the terminal plate (Text-fig. 8).

I believe this may have been the feature to which Sladen referred.

(*b*) Dorsal Plates, Ventral Plates, Lateral Plates, Vertebrae (ambulacrals).—I have little to add to Fewkes's account of the development of these plates, which is completely confirmed by observation on the present species. The ventrals form first from a bluntly trifid spicule, one point of which is directed adorally. Then follow the laterals, which develop rapidly and soon exceed the ventrals in size. Finally, their outwardly growing edges almost meet eventually in the ventral midline above the ventral plate and on the upper side below the dorsal plate, which is the last to appear. In the meantime the internal vertebrae are laid down. These appear first as a pair of Y-shaped trifid spicules (Text-fig. 10), the two shorter limbs of the Y directed adorally. In their development the adoral end of each grows outward and becomes closely appressed to its fellow (not usually fused to it as Ludwig's account states for Amphiura). Later, the aboral end grows outward and also comes into close relationship with its fellow. In the most developed segment (i.e. the first) of my oldest specimens the vertebra has assumed the form of a pair of calcareous rods adpressed at their adoral and aboral ends, bow-shaped with the convex side of each bow directed outwards so as to leave a space vacant in the middle (Text-fig. 10, *Vert. I*,). This, of course, is the primitive 'Ophiohelis' condition.

Fewkes records that in Amphiura the rudiments of the vertebrae are not always Y-shaped, but sometimes only simple needle-shaped spicules. He figures such rudiments. I have not been able to detect such spicules in my preparations. The spines borne on the lateral plates (one pair on each plate in



Text-fig. 8.

I–III, Development of the terminal plate.
IV, V, Development of the spine.

the young form) develop from two or three rather irregular simple spicules which fuse to form the conical (and apparently at this stage, hollow) structures shown in Text-fig. 8, IV and V, and Pl. 22. I mention this here and will have occasion to refer to it again when describing the development of the tooth, as it has been suggested that the teeth are derived from modified spines. That the spines develop in this way has not been recorded in the literature available to me.

3. The Plates of the Oral Skeleton.

(*a*) Oral shields.—These have been described already as part of the original calycinal system.

(*b*) Adoral plates.—These, like the plates of the arm, originate as branched spicules (Pl. 22). Each bears one spine. They lie to either side of the interradially placed oral shield, and are held to represent the second pair of the adambulacral series (of which the first pair of laterals are held to be the third pair). With further development each adoral plate assumes a triangular outline (Pl. 22, *Ad. 2*). The interradial face is convex and lies against the adoral apex of the oral shield for part of its length, and against its fellow adoral of the other side for the rest of its length. The two other sides are concave. Against one, the more aboral, the first podium is accommodated, lying between the adoral and the first ventral. The remaining side of the adoral is opposed to the aboral border of the semi-angular plate of its side.

(*c*) The Oral Plate.—The oral plate arises in development by the fusion interradially of two semi-angular plates, each derived from one side of the interradius. In all my preparations the two semi-angulars are still distinct, so that the oral plate proper is not yet formed (Pl. 22). At the adoral apices of the semi-angulars of a pair, the torus angularis is developed. Each semi-angular plate is itself composed of two plates, (*a*) a more adoral element, which is a member of the first pair of adambulacrals, and (*b*) a more aboral element considered by Ludwig to represent a member of a second pair of ambulacrals, but which Fewkes suggested might really be a member of the first pair of the ambulacral series.

Thus the final oral plate is derived from four plates—two ambulacrals and two adambulacrals.

In the case of Amphiura, Fewkes's figures and text seem to suggest that the ambulacral and adambulacral elements of each semi-angular arise quite independently, and only later become united to form the semi-angulars. But in the present species the semi-angular appears right from the first as a calcareous network apparently in one continuous mass. When examined under ordinary light this appearance is misleading, as

it leads one to suppose that only the adambulacrals are present. When examined under polarized light, however, it is found that the apparent single adambulacral plate is in reality composed of two zones which extinguish independently at different angles. It is clear that only the ambulacral elements will be concerned in the later fusion of the two semi-angulars, for the ambulacrals are quite separated from each other by the aboral ends of the adambulacrals. In the later stage (shown in fig. 35, Pl. 22) it will be seen that the two adambulacral regions of each pair of semi-angulars are in close contact, but not fused: already the future oral plate is assuming the typical form which has led some authors to call it the 'V-shaped plate'.

The oral plates are related to their neighbouring plates as follows: on the adoral aspect they border the torus angularis, next to be described. On their radial borders they are in relation with the peristomial plates in the young form, but at a succeeding stage these latter plates migrate dorsally (see p. 429), leaving the oral plate to constitute the entire base of each triangular jaw-like region of the mouth.

As mentioned above (p. 416), the crystalline axes of the two component elements of each semi-angular plate are inclined at an angle which is constant within certain limits. Twelve readings obtained with a graduated rotating stage show that the average angle of inclination is about 35°, the limits being 30° and 40° respectively.

(*d*) The Torus angularis and Teeth.—Owing to their extreme minuteness and transparency at their earliest appearance, the study of these structures is difficult without the use of polarized light.

Fewkes's account, the most satisfactory available to me, briefly describes the development of these plates in the following words (1887): 'These structures arise later than the first pair of adambulacral plates, but develop quite early in the growth of the young Amphiura. They form as independent calcifications. The torus is at first an elongated plate or bar, which later becomes semicircular. In fig. 20 this plate is represented as perforated and reticulated. It appears that the teeth are not separate centres of calcification but grow

out directly from the adoral region of the torus. The calcareous deposit which enters into their formation has the form at first of a reticulated perforated triangular plate.' (The spaced words are mine.) Fewkes's figures, excellent in other respects, do not show these structures very clearly.

J. P. MacMurrich (1906) contradicts Fewkes's account in the following words. The oral plate is stated to be 'furnished with a number of stout projections, the palae angulares (i.e. the teeth) whose bases generally fuse to form a supporting plate, the torus angularis'. (The spaced words are mine.) No figures or specific examples are given to support this statement. The question is not dealt with by any other authors known to me.

Of the origin of the tooth and torus angularis in the present species I am able to give the following account:

The Tooth.—The tooth undoubtedly originates quite independently of the torus. The rudiments regularly comprise no less than nine separate centres of calcification, these being so grouped as to givee vidence of a pronounced bilateral symmetry (Text-fig. 9). The axis of symmetry is the interradius. The elements are so arranged as to form parallels to the vertical axis of an isosceles triangle, whose base abuts on the torus. For these structures I propose the general term 'Dental spicules', which may be classified as follows:

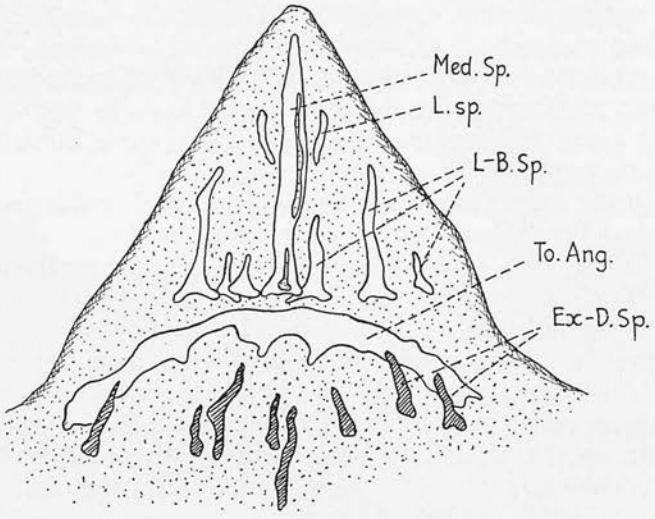
(1) The medial spicule.—This occupies the central axis of the tooth (Text-fig. 9, *Med. Sp.*) and is the largest element. In all my preparations the structure appears unpaired, but from certain longitudinal fissures which occur in this spicule, I have little doubt that it originates from a pair of parallel rudiments which early fuse at their extremities.

(2) The lateral spicules.—A pair of symmetrically disposed spicules of small size but regular occurrence are seen near the adoral apex of the medial spicule, one on either side (Text-fig. 9, *L. Sp.*). These are the most adoral elements of the tooth, and are quite separated from the remaining structures which can be collectively classified as—

(3) The latero-basal spicules.—Of these there are generally three pairs, symmetrically placed along the base of the

triangle, on either side of the medial spicule. On each side one of the latero-basals is more developed than the other two, reaching a length equal to about half that of the medial spicule. Which latero-basal is so developed varies from one tooth to another (Text-fig. 9, *L.-B. Sp.*).

It will be noted that, in contrast to all the other spicular



TEXT-FIG. 9.

Early rudiments of the tooth. *Med. Sp.*, medial spicule; *L. Sp.*, lateral spicule; *L-B. Sp.*, latero-basal spicule; *To. Ang.*, torus angularis; *Ex-D. Sp.*, extra-dental spicule.

rudiments of skeletal plates, these spicules are characterized by their simple uniaxial form—instead of being triradiate as might be expected.

Later Development of the Tooth.—The isolated elements above described consolidate to form the tooth by uniting first along the base of the group, i.e. the aboral border, and then round the remaining two sides—thus forming a triangular plate with an indented margin on its two radial sides, and perforated by elongate fissures between the original spicules.

Later development results in the complete obliteration of all fissures and the production of the tooth-like structure of the adult.

In the specimens observed by the writer only one tooth had developed—as was the case in the young Amphiuras described by Fewkes. It is presumed that the teeth which later develop in linear series, on the dorsal aspect of the first, will originate in the same manner.

As has been noted above, the crystalline axes of the dental spicules correspond with their long and short morphological axes, being parallel to the axis of symmetry of the group.

Evolution of the Tooth.—It is agreed that neither the teeth nor the torus angularis can have been derived from modified ambulacral or adambulacral ossicles of the arms. Two suggestions as to the origin of the teeth appear to have been put forward: (1) They represent later superficial additions; (2) They represent spines (presumably the spines that would have been carried by the ambulacral plates which entered into the formation of the buccal skeleton).

When considered in the light of the developments described above of the spine and of the tooth, the second theory would seem untenable, as there is no obvious similarity between these two structures at any stage in their development. On the other hand, the first theory, that they represent superficial additions, is supported by the fact that in the neighbourhood of the developing tooth, on its aboral side, there are to be seen a number of irregular, approximately needle-shaped spicules lying near the surface. I suggest for them the general term 'Extra-dental spicules'. These are shown in Text-fig. 9. They have a very rough approximation to a bilateral arrangement, but are irregular in shape and size, and variable in number. It is conceivable that the regularly arranged rudiments of the primitive tooth could have been derived from spicules such as these.

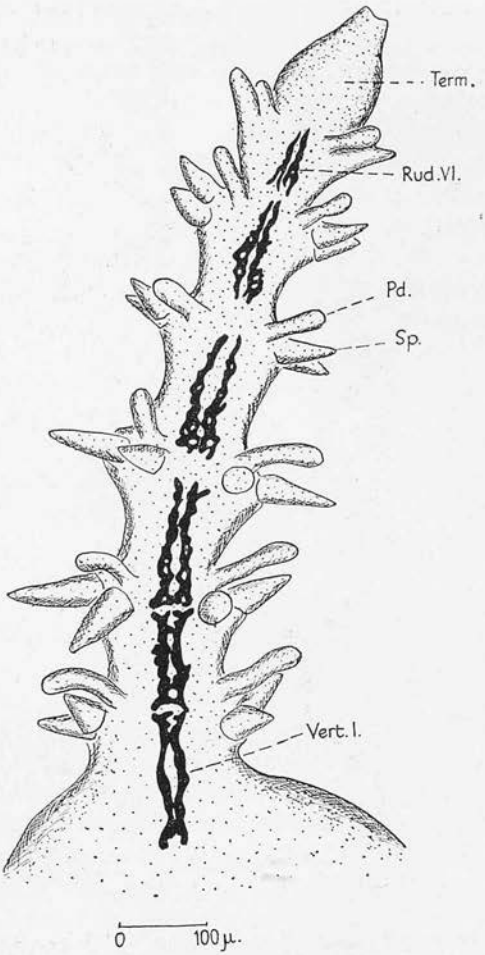
The Torus Angularis.—In the preparations studied the first rudiment of the torus appears as an elongated, transverse bar, bow-shaped, with its convex side directed adorally towards the base of the developing tooth (Text-fig. 9, *To. Ang.*). The two extremities of the bow are directed towards the radial

borders of the adambulacral zone of the semi-angulars. Later growth results in the formation of an ellipsoidal plate, of a curvature such that the original curved bar forms an arc of its circumference, on the adoral side. The greater part of this plate overlies the adoral extremities of the semi-angulars of its interradius. It consolidates into a well-defined platelet earlier than all the other plates (see fig. 35, Pl. 22), and at the stage of seven arm-segments it presents a regular outline, and its perforations are much smaller than those of the surrounding plates. By focusing up and down it is seen that the adoral margin of the plate at this stage is considerably thickened, this thickening corresponding in position to the original curved bar.

(*e*) The Peristomial Plates.—These structures, regarded by Ludwig as representing the first pair of ambulacral plates (i.e. the two halves of a first vertebra), and by others as being really superficial additions, appear early in the development as a horseshoe-shaped, scattered group of spicules (Pl. 22, *P. P.*) which later unite to form two bow-shaped plates. They occupy a radial position between two sets of semi-angulars, and their convex edges are directed outward, i.e. interradially. These plates when still further consolidated assume a very typical form (Pl. 22, *P. P.*), having on their interradial borders a strong, imperforate, calcareous zone forming a well-marked boundary to each plate where it abuts on the neighbouring semi-angular. At this stage the peristomial plates occupy the aboral extremities of the buccal fissures.

(*f*) The Definitive Skeleton of the Adult.—Although the identity of the present species is not yet known, the general skeletal characters of adult ophiuroids are fundamentally similar.

The oral shields are carried by the growth of the disc into a ventral position, and come to lie between the two adoral plates. The semi-angulars in Pectinura are obscured by calcareous granules of the epidermis. The borders of the semi-angulars develop oral papillae on their radial aspect, but their development is not known. The ventrals, dorsals, and laterals of the arm consolidate to form a regular interlocking armour, the laterals bearing spines. Internally, the

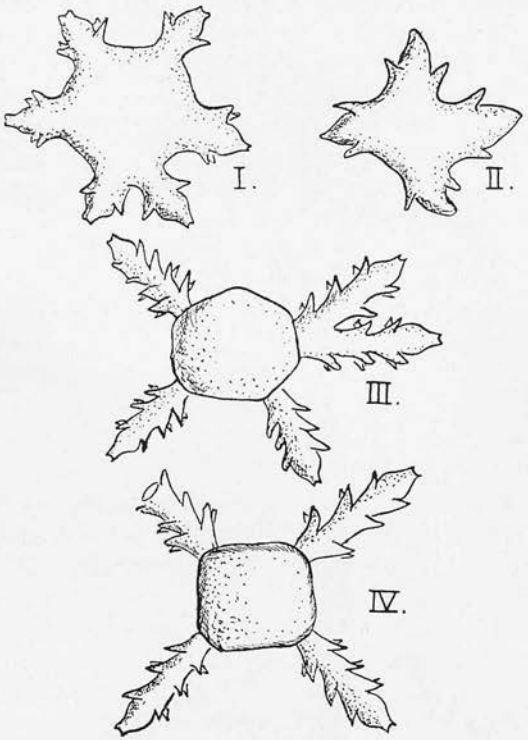


TEXT-FIG. 10.

Stages in development of vertebrae. *Term.*, terminal segment; *Rud. VI*, rudiments of sixth vertebra; *Pd.*, podium; *Sp.*, spine; *Vert. 1*, first vertebra, in the 'Ophiohelis' condition.

madreporite is formed by an oral shield distinguished by a groove on its dorsal side. The peristomial plates migrate upwards and apply themselves to the dorsal surfaces

of the semi-angular plates. The number of teeth is increased by additions dorsally to the first. The vertebral rudiments unite and form flattened plates. The torus comes to form a vertical bar supporting all the teeth.



TEXT-FIG. 11.
Monstrosities (see text below).

IX. MONSTROSITIES.

During the progress of the work a number of variant forms and monstrosities were noted.

The commonest type of variation was a simple meristic change in the number of radial plates. These were often noted

to be six in number instead of five. The other features of the animal remained unaffected.

Meristic variation in the number of arms occurred to a lesser degree, and was associated generally with dwarfed development. A six-rayed individual, of very retarded development, is figured in Text-fig. 11, I; it was taken from a group, the average individuals of which had reached the stage of five arm-segments. Apart from the arms, the symmetry was pentamerous.

A four-armed individual of very stunted development is shown in II of the same figure. It was a member of a group which had on the average reached the four-arm segment stage. Text-fig. 11, IV shows an individual of normal size for its group, but having only four arms. The jaws and other features were pentamerous.

Text-fig. 11, III shows an individual having three normal arms and one bifurcated arm, the bifurcation affecting the second segments (see p. 436).

X. Discussion and Conclusions.

The variation in position of the first cleavage-plane is most remarkable, particularly in an Echinoderm. It is greatly regretted that no method could be discovered by which the nature of the corresponding nuclear changes could be studied. Such a method may in due course be developed. When the first and more usual manner of cleavage is followed, in which the two first blastomeres are approximately equal, the process evidently corresponds with the general echinoderm mode of development. But when the two first blastomeres are unequal, the only parallel case in Echinoderms known to the writer is that described by Apostolides (1882) and Russo (1891) for Amphiura squamata.

Apostolides, whose paper I have not been able to obtain, evidently recorded that the first cleavage in Amphiura is markedly unequal. He was led to believe that the larger of the two first blastomeres then segmented to form three cells, the total number of blastomeres thus being brought to four. This account, if true, seems almost identical with what is believed to occur in the present instance.

However, Russo states that he believes this is not the case. He confirms the fact that the first cleavage is unequal. But regarding the succeeding cleavages he states that the larger blastomere divides in a plane normal to the first cleavage-plane, to give an embryo of three approximately equal blastomeres. He states that a succeeding cleavage brings the number to four, but gives no details of the process. He points out that his description contradicts that of Apostolides.

A noteworthy difference between Amphiura and the present species is provided by the polar bodies. While these are large in the former species, they are either so small in the latter as to have degenerated before the earliest stage observed by the writer, or are cut off before the formation of the egg-membrane. Occasionally small masses of cytoplasm and yolk-granules are seen within the egg-membrane, but whether these are the remains of the polar bodies I cannot say. Their occurrence is irregular.

The early differentiation into micromeres and macromeres, showing the polarity of the egg and the previous existence of a prelocalization, is very noteworthy. In this respect this species differs from Amphiura, and, indeed, from other echinoderms. The small size of the blastocoel relative to that of the egg is undoubtedly correlated with the large amount of yolk present. With the smallness of the blastocoel the reduced form of invagination automatically follows. Then, to compensate for the reduced invagination, the long process of epibolic ingrowth of the micromeres (epiblast) takes place. The greater amount of epiboly on two sides, forming parallel crests, is notable in the early stages of the process. All these processes are without parallel in existing known echinoderms, but are strongly reminiscent of the development of other animals with yolky eggs. The blastula, with its micromeres and megameres and meniscus-shaped blastocoel, and the blastomeres without cilia, may be compared with the corresponding stage in the Frog. The extraordinarily reduced archenteron can also only be paralleled in other groups where yolky eggs occur. The blastopore occupies the position of the future mouth. This is, of course, contrary to the usual fate of the blastopore in ophiuroids since it normally gives rise to the anus of the larva. No larva is ever developed

in this instance, and an ophiuroid has no anus apart from its larval one; consequently no special significance seems attachable to the fate of the blastopore.

In the case of Amphiura the blastopore (which has an entirely different origin from that described in this species if Russo's and Apostolides's accounts are correct), is stated to give rise to neither the mouth nor the anus of the reduced larva, but to disappear early in development.

In Amphiura squamata it is stated that the endoderm and ectoderm arise by delamination of the cells of the blastula. Metchnikoff (1869), who first studied this species and who did not follow the formation of the germ layers, assumed that invagination occurred. Apostolides (1882), who later worked on this species, believed that the layers arose by delamination. Fewkes (1887) did not observe the process but remarks—'It would not seem strange if, in the possibly abbreviated development which is found in Amphiura, a true anal opening never forms, and that the primitive gastrula cavity is formed not by invagination but by delamination.' Russo (1891), the next worker, states definitely that this is the case, and compares Amphiura with Gergonia and Hydra. MacBride (1914), who had not observed these stages, states—'Such statements as these are improbable in the highest degree.' The writer has no comment to make, seeing that delamination does not occur in the species studied by him; but it is to be hoped that some European or American worker with access to material will soon clear up the matter.[1]

In Ophiura it is stated by Grave that an invagination of a solid mass of cells takes place, which becomes hollowed out so as to form an archenteron. In Ophiothrix, described by MacBride, a free-swimming, ciliated blastula invaginates to form a gastrula with an archenteron, in the usual way. Evidently, therefore, the only ophiuroid development which at all resembles the present species at this stage is that of Ophiura —which it will be recalled has a yolky egg—and even here the resemblance extends only to the invagination of a solid mass of cells.

[1] The writer is now working on this subject in Britain.

I believe that the present species is unique among known Echinoderms in having completely lost all trace of a larval stage. At least no mention is made of such a fact in any of the literature available to me.

This is the more remarkable in view of the fact that the species is oviparous. One normally associates suppression of larval stages with viviparity. The ontogenetic explanation of the fact would appear to be provided yet again by the hampering effect of a yolk mass. But it is not clear that this is the phylogenetic cause. The non-expression during development of a character (Lipopalingenesis) is normally intimately associated with the phenomenon of Tachygenesis. But it seems clear, from a comparison with the rates of development of other ophiuroids, that far from being tachygenetic, the present development is retarded. The first cleavages, for instance, are slow—the gastrulation takes several days to complete—and the skeletal system is delayed in its appearance. Thus, instead of exhibiting acceleration, the present development is distinctly bradygenetic. Why, then, should the larval stage be omitted and the radial symmetry of the adult be the only one ever to appear?

The writer would suggest two possible explanations—these being, of course, entirely hypothetical.

It is possible that the ancestral stock of the species may at some time in the past have been viviparous. The conditions in that case being such as to render the development of a larva entirely useless, a process of cumulative reduction in development of the larval stage could well set in. A stage in such a process would be illustrated by Amphiura squamata to-day, with its transitory reduced larva. If the bioseries be taken to its limit, the final stage is reached at which no larval form whatever is formed. Having once been lost, a character seldom reappears in evolution. Thus, if later such ophiuroid stock were to cease to be viviparous, a development similar to the present would take place.

The second explanation is suggested by the presence in New Zealand of a large number of biological types which give evidence of the severe conditions which prevailed in this country during the recent Ice Age. These types, though now living in

easy conditions, still exhibit modifications evolved for a colder climate. Larval forms are regulated by climatic conditions. In tropical regions they reach their fullest expression, often in most extravagant forms. In severe climates they tend to be suppressed. The writer suggests that it is not fantastic to attempt to relate the loss of the larval stage in this animal with the severe Ice Age conditions above referred to.

Having lost its larval stage, and not ever possessing anything but a vestige of the archenteron, the derivation in ontogeny of the coelom by splitting in a mesenchyme mass is not surprising.

That a similar process should be said to occur in Amphiura squamata would seem to point to viviparity, with corresponding reduction of the larva, as being a primary cause. In the present species, however, it is likely that the immediate factor controlling the process in ontogeny is again to be found in the yolk mass of the gut. For purely physical reasons the presence of such an inert mass of material in the cells of the hypoblast would render the cutting off of enteric pouches an excessively slow process. Certainly it is impossible to relate the simplified mode of development with a corresponding simple ancestor. It must, from the evidence of the other Echinoderms, have been arrived at by a process of secondary simplification. As MacBride (1914) points out—'What preserves a continuous record in ancestral history is the continuity of functional activity. If this be interrupted, all sorts of aberrancies may occur.' In this case it is not the functional activity that has been interrupted. Rather it has been carefully preserved, but in order to do so aberrancy in developmental processes resulted, owing to changed conditions in the cells themselves, or their external environment.

While studying the development of the present species the writer was struck by the fact that so frequently corresponding organs arose almost simultaneously. This, of course, is no doubt common to all Echinoderms, but in the present instance the following cases may be mentioned:

The rudiments of the first podia appear simultaneously; the developing arm buds grow out symmetrically—and therefore at the same rate: the centro-dorsals (and other skeletal groups)

keep pace with one another in development; when the rudiments of the teeth are first laid down there is apparent a co-ordination in the appearance of even the minutest spicules; spicules which are to unite to form the same plate have their crystalline axes parallel, while yet still separated. In all these cases where corresponding organs keep pace with each other, it is to be noted that their radial distances from the centre of the animal are equal. This fact surely is significant, and seems to suggest that all these processes are to be explained in terms of hormonic activity. By analogy with vertebrate development, one would tend to look to the region of the blastopore when seeking a possible organizer. The blastopore occupies the centre of the ventral surface of the disc, and thus is equidistant from corresponding points of the animal. It is suggested tentatively that from the tissues of this region may be liberated the substances which control the major features of the ontogeny. If this were so, the substances travelling outward along the radii and interradii would arrive at corresponding regions at corresponding times, and thus homologous organs in the different arms would arise simultaneously.

Again, it would seem reasonable to suppose that the early outgrowth of undifferentiated arm-buds at five points on the periphery is caused by one hormone; while the later differentiation of each arm is to be attributed to a second hormone, liberated later than the first. If this is the case, we can explain the curious monstrosity shown in Text-fig. 11, III as due to the delayed action along one radius of the first hormone, differentiation by the second hormone (to the extent of one segment) having already set in before the belated development of the fifth arm began.

Conclusions.—The present ophiuroid is a species which has had the earlier stages of its development profoundly altered by some factor or factors in the course of its evolution. The immediate ontogenetic factor would appear to be related to the yolk mass within the egg. The alteration has greatly influenced the process of gastrulation; it has completely effaced the larva from ontogeny; and has resulted in the formation of the coelom later in development, and by the unusual method of splitting.

The parallels between the recorded development of Amphiura squamata and the present species suggest that other similar cases will be found.

The view which required every species to recapitulate in its ontogeny its ancestral stages has no real claim to such universality, as is yet once again illustrated by its inability to explain the present instance. The criticism of the previously recorded instance of Amphiura squamata emphasizes more forcibly the grave shortcomings of the Recapitulation Theory in its original form. This view was bound to regard cases such as these (when it regarded them at all) as quite exceptional, and coined for their anomalies the term 'caenogenetic'. When one notes the fact that two out of four known Ophiuroid developments, i.e. 50 per cent., are 'exceptional', it becomes a matter for discussion as to which 50 per cent. is 'normal'.

As de Beer (1930) points out, the importance of cases such as the present one, where the older animal is so similar to others of its class, while the young form is so markedly dissimilar to the other young of its class, is that it illustrates the fact that evolution can, and does act upon the early stages of development. Moreover, it may act without leaving its mark on phylogeny—for only the adult forms are concerned in phylogeny. It is an example of that type of evolution which de Beer has termed 'clandestine'.

It is stimulating to speculate on what extraordinary animal might arise should a species such as the present come under the influence of paedogenesis.

XI. Summary.

1. The first cleavage may be either equal, or markedly unequal; when it is equal the next segmentation affects both blastomeres; when it is unequal the larger blastomere is believed to give rise to three cells, and the smaller remains undivided till the next cleavage.

2. At the eight-cell stage there are two quartets of blastomeres. The upper quartet, micromeres, occupy the animal pole. The lower quartet, macromeres, occupy the vegetal pole.

3. The blastula comprises micromeres and macromeres, and

the blastocoel is small and becomes eccentric. No cilia are developed.

4. The gastrula is formed by the shallow invagination of the macromeres, accompanied by an extensive process of epiboly affecting the micromeres. More marked epiboly of cells on two sides of the blastomere produces in the early stages two crests which later disappear. These may indicate a trace of bilateral symmetry. Epiblast comes to lie on solid mes-hypoblast. The archenteron is transient, and gives rise to no structures. The blastopore occupies the position of the definitive mouth.

5. No larva ever forms, nor is there any vestige of a larval stage.

6. The solid gastrula is converted into the adult by assuming a radial symmetry directly, with no intermediate bilaterally symmetrical form, unless the two epibolic crests are regarded as vestiges of larval symmetry.

7. The podia appear as solid outgrowths, in which the hydrocoelic cavity develops by splitting.

8. The definitive enteron appears as a split extending upward from the ventral surface through the solid hypoblast.

9. The young ophiuroid leaves the egg before the appearance of the general body cavity, and moves about, but does not at first take food.

10. The general coelomic body cavity and the perihaemal cavity develop by splitting in a mass of mesenchyme derived from the outer layers of mes-hypoblast.

11. The formation of the skeletal system is delayed till the stage of between two and three arm-segments.

12. The development of the skeleton follows closely that described for Amphiura squamata.

13. The tooth is shown to originate independently of the torus angularis; its rudiments comprise nine symmetrically disposed spicules.

14. The terminal plate arises later than the radials, and has a distinctive 'primitive structure'.

15. The spine is shown to have a different development to that of the tooth, and therefore would seem to have no connexion with the latter in phylogeny or ontogeny.

16. It is suggested that the aberrant early stages are to be correlated with the retarding effect of the yolk mass present in the egg during ontogeny. The aberrant features may have had a different origin in phylogeny.

17. It is suggested that the simultaneous appearance in ontogeny of homologous organs situated at equal radial distances from the centre is to be explained in terms of hormonic activity.

18. It is concluded that evolution has considerably affected the early ontogeny without leaving its mark on phylogeny. The adult thus conforms to its class, the young form does not.

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EXPLANATION OF PLATES.

Plate 20.

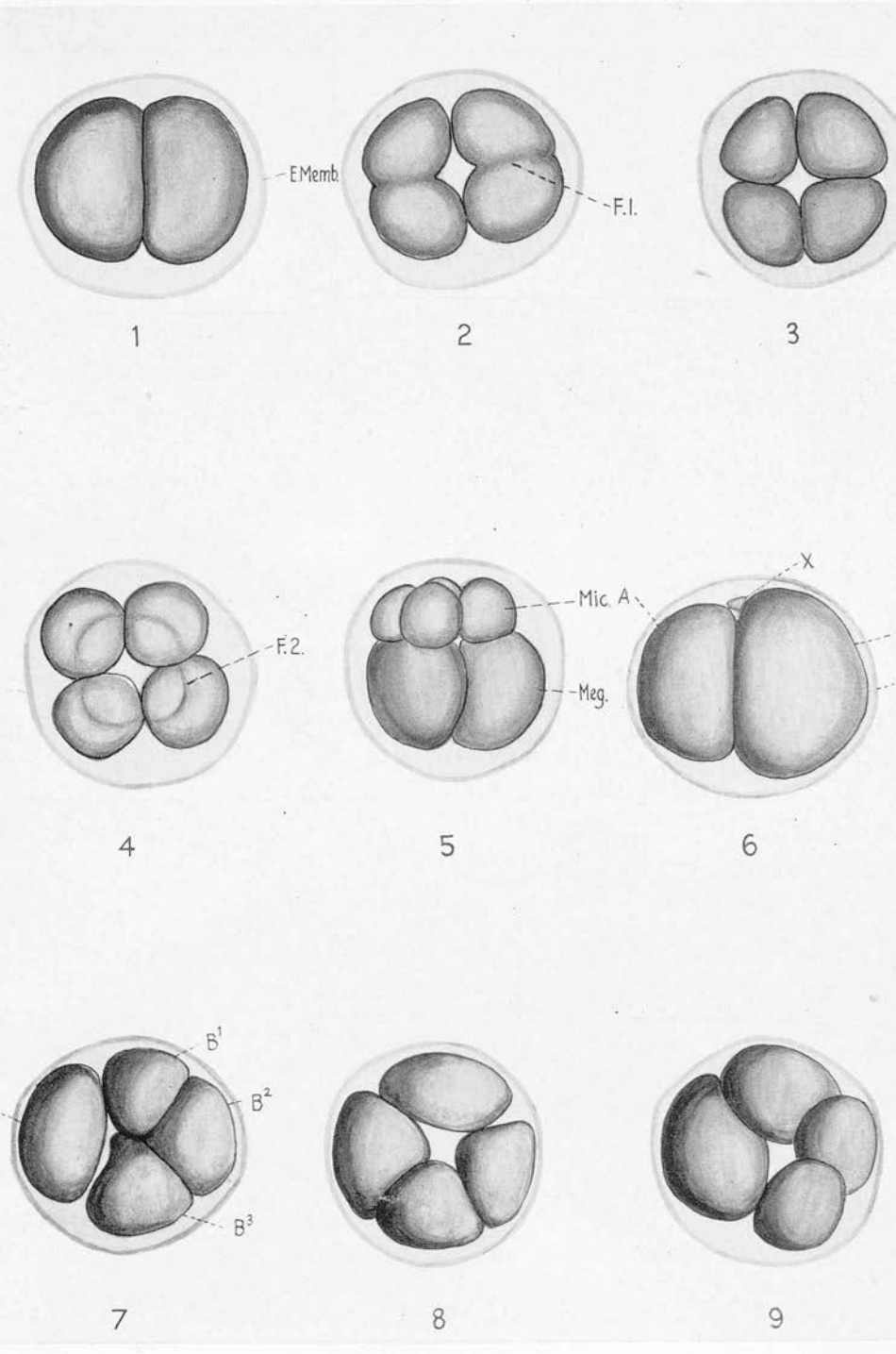
Fig. 1, two-cell stage; fig. 2, beginning of second cleavage; fig. 3, early four-cell stage; fig. 4, late four-cell stage showing furrows of the third cleavage; fig. 5, eight-cell stage; fig. 6, two-cell stage with unequal cleavage; fig. 7, early four-cell stage resulting from 6; figs. 8–11, divisions subsequent to 7; fig. 12, eight-cell stage; fig. 13, morula; fig. 14, blastula; fig. 15, early gastrula; fig. 16, early gastrula showing epibolic crests; fig. 17, same viewed from vegetal aspect. Drawn by reflected light. *A*, lesser blastomere; *An. P.*, animal pole; *B*, greater blastomere; B^1, B^2, B^3, cells supposed to have been derived from *B*; *Blp.*, blastopore; *E. Memb.*, egg membrane; *Epib. Cr.*, epibolic crest; *F. 1*, furrow of second cleavage; *F. 2*, furrow of third cleavage; *Meg.*, megameres; *Mic.*, micromeres; *X*, remains of polar bodies?

PLATE 21.

Fig. 18, vertical section through blastula; fig. 19, same, invagination beginning; fig. 20, vertical section of blastula cutting epibolic crests transversely; fig. 21, vertical section early gastrula; fig. 22, vertical section, early gastrula, cutting the median tip of one crest, plane of sectioning to one side of median plane of egg; fig. 23, gastrula after obliteration of blastocoel; fig. 24, first appearance of radial symmetry; fig. 25, same, from ventral side; showing 'rosette' form; fig. 26, appearance of the podia; fig. 27, same, from ventral side; fig. 28, newly emerged, dorsal view; fig. 29, same stage, ventral view; fig. 30, 'Asterina' stage, dorsal view; fig. 31, same stage from side; fig. 32, stage showing first arm-segment; fig. 33, stage showing seven arm-segments. Figs. 18–23 from stained preparations; figs. 24–33 from life. *An. P.*, animal pole; *Arch.*, vestige of archenteron; *Blc.*, blastocoel; *Blp.*, blastopore; *Epib. Cr.*, epibolic crest; *Epib. R.*, region of epiboly; *Epibl.*, epiblast; *G.*, gut, with localized yolk; *Hypobl.*, hypoblast; *Int. Gr.*, interradial groove; *J.*, jaw; *Meg.*, megameres; *Mic.*, micromeres; *Mo.*, mouth; *N.*, nucleus; *Oblit. Blc.*, obliterated blastocoel; *Per. Z.*, clear peripheral zone; *Pod. 1, 2, 3*, first, second, and third podia; *Pod. Rud.*, rudiments of podia; *Ppl. Memb.*, protoplasmic membrane; *Ra.*, radius; *Rud. J.*, rudiments of jaws; *Rud. R.*, rudiment arm; of *E. Memb.*, egg membrane; *Sg. 1*, first segment; *Sp. 1, 2, 3*, first, second, and third spines; *Term.*, terminal segment; *Veg. P.*, vegetal pole; *Vent. S.*, ventral surface.

PLATE 22.

Fig. 34, early rudiments of the skeletal plates; fig. 35, skeletal system, later stage. Ventral views, drawn from cleared mounts, under polarized light. *Ad. 2.*, second adambulacral (= adoral plate); *L. 1, 2*, first and second laterals; *L.-B. S.*, latero-basal spicule; *L. S.*, lateral spicule; *M. S.*, medial spicule; *Mo.*, mouth; *Or. S.*, oral shield; *Pd. 1, 2, 3*, first, second, and third podia; *P. P.*, peristomial plate; *S. Ang.*, semi-angular; *Sp. 1, 2, 3*, first, second, and third spines; *T.*, tooth; *To.*, torus angularis; *V. 1, 2, 3*, first, second, and third ventrals.



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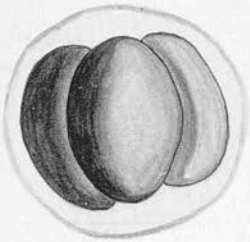

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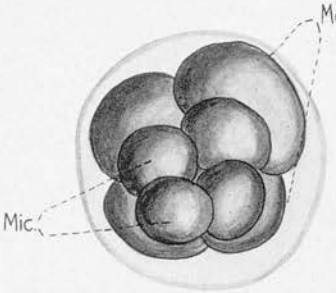

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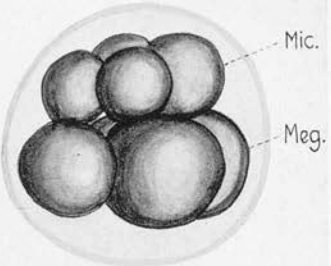

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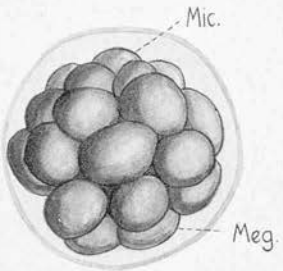

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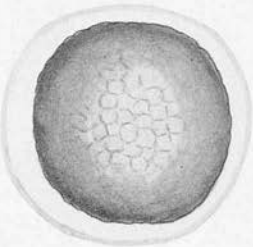

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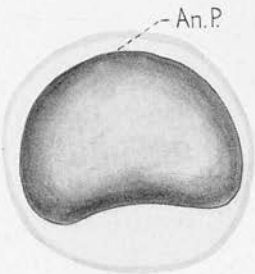

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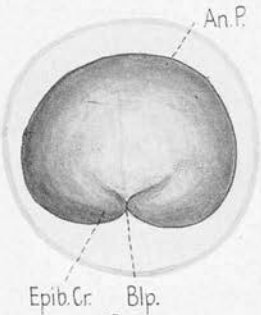

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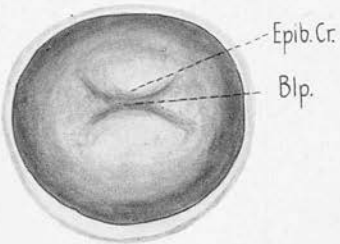

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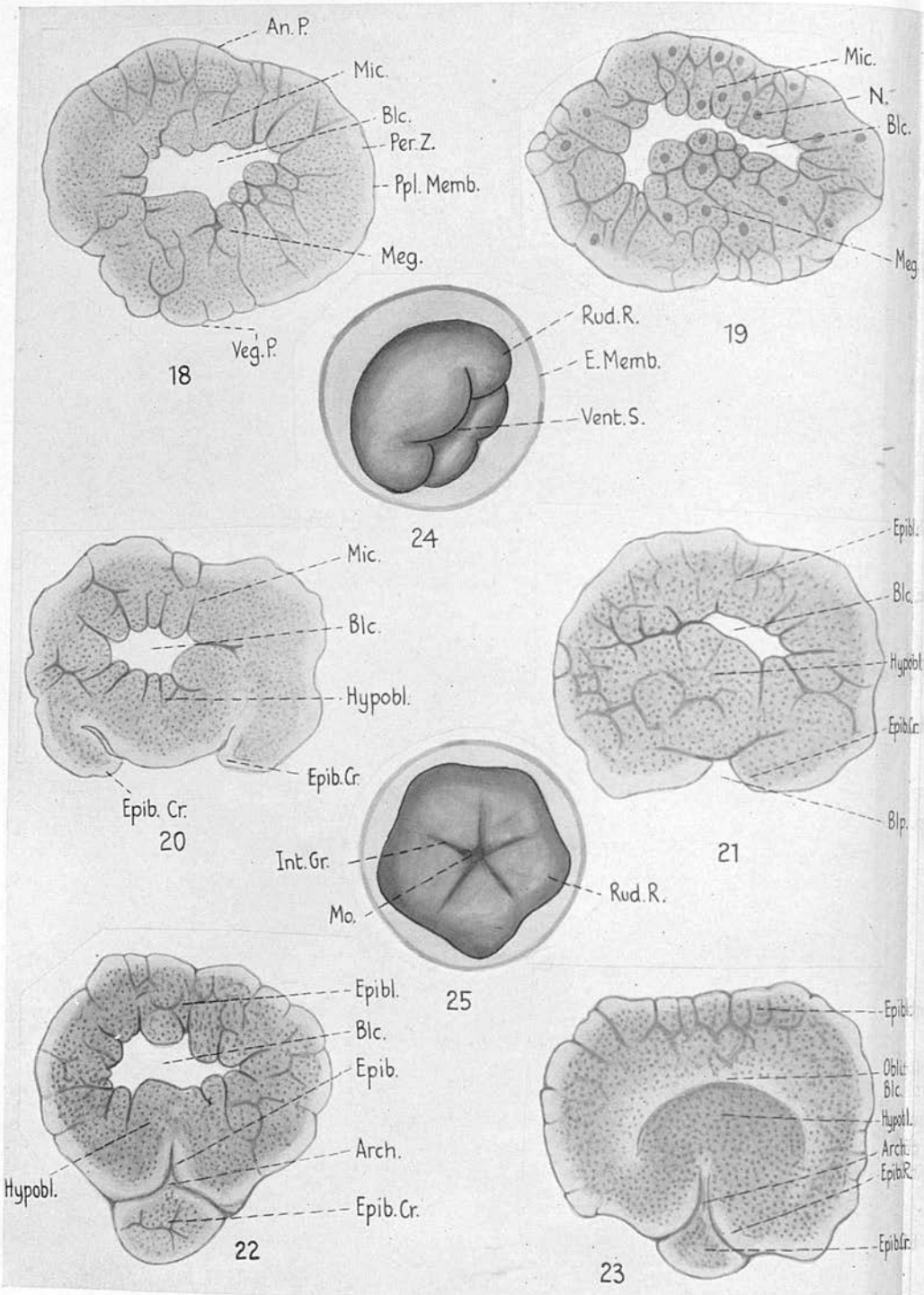
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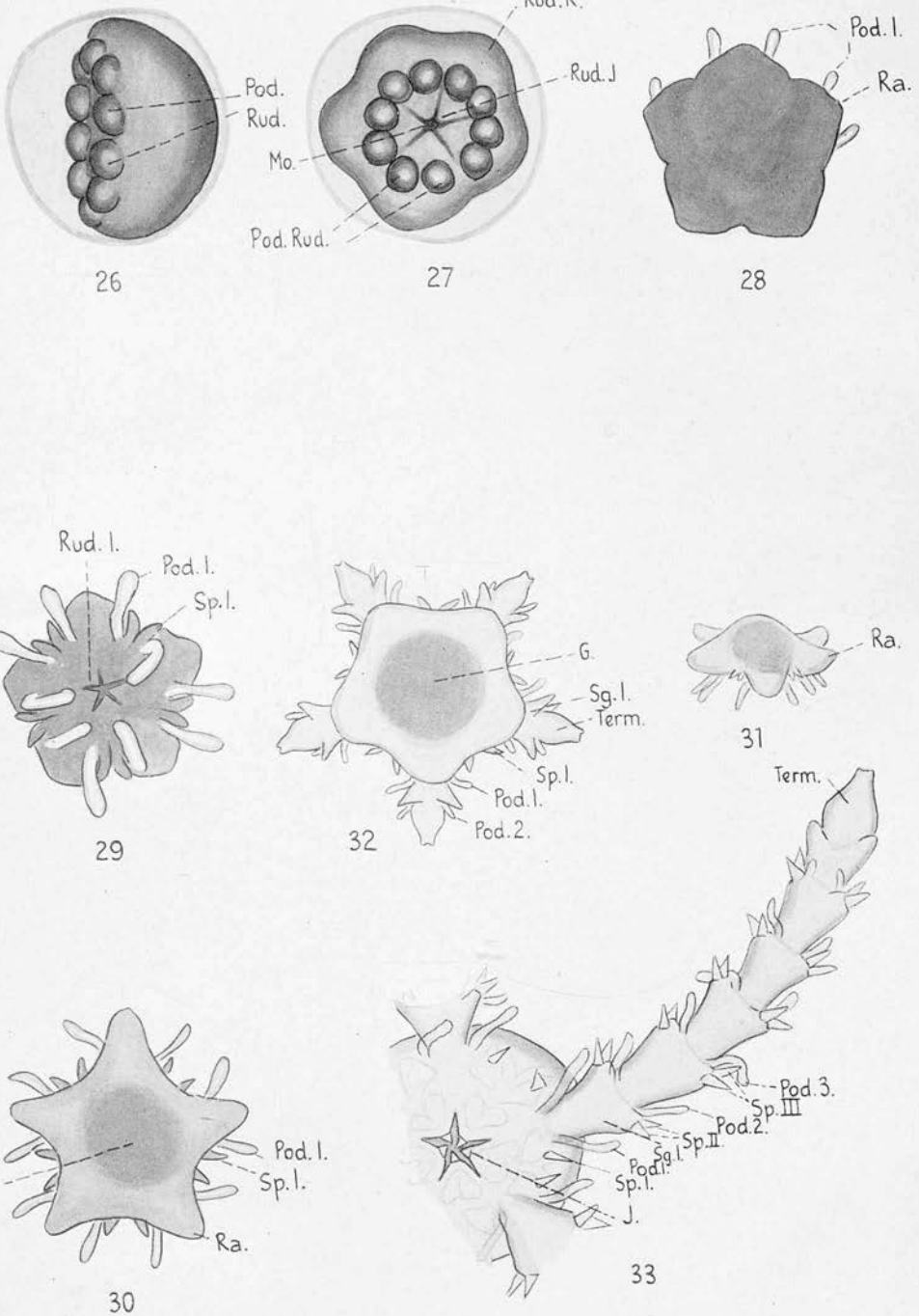
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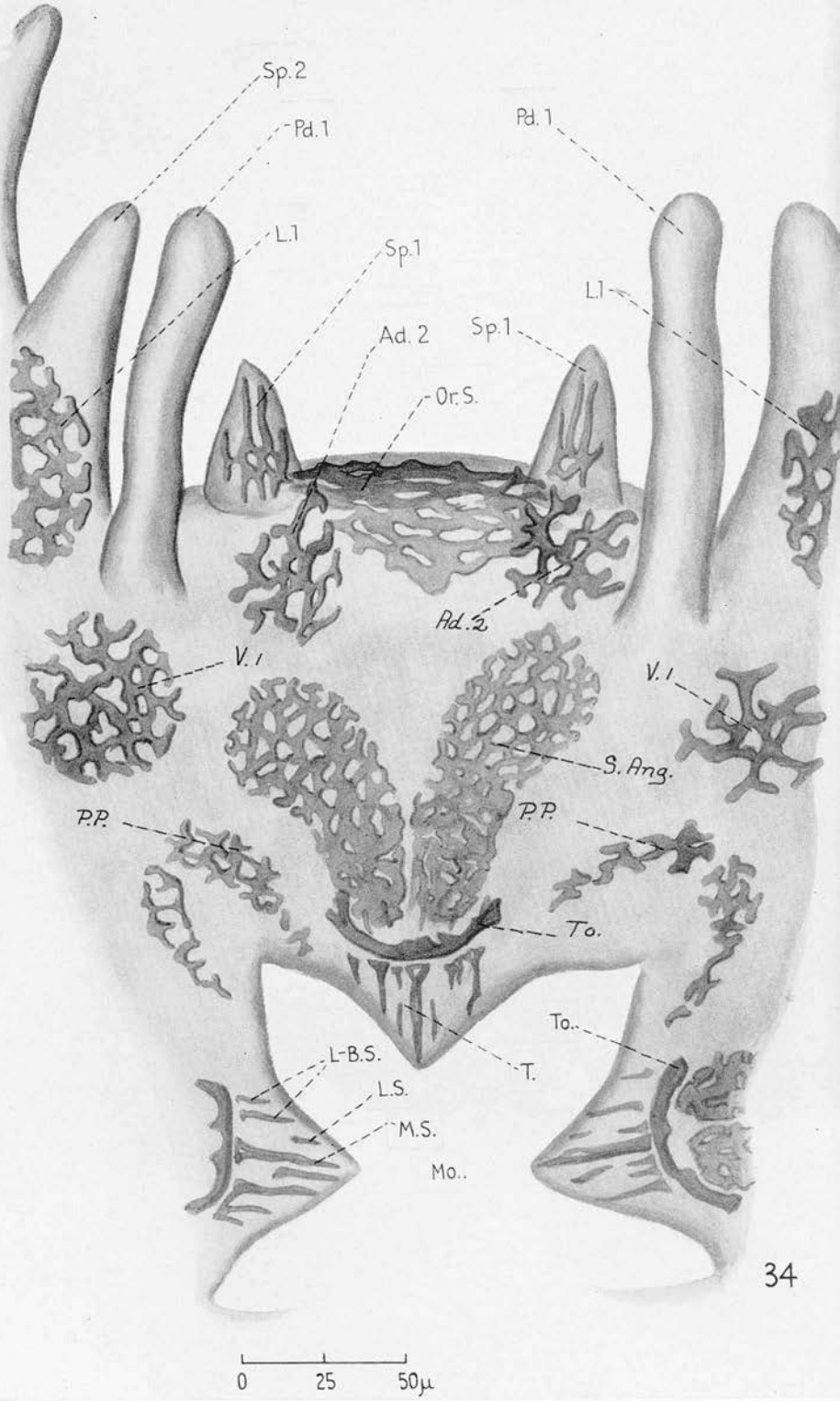

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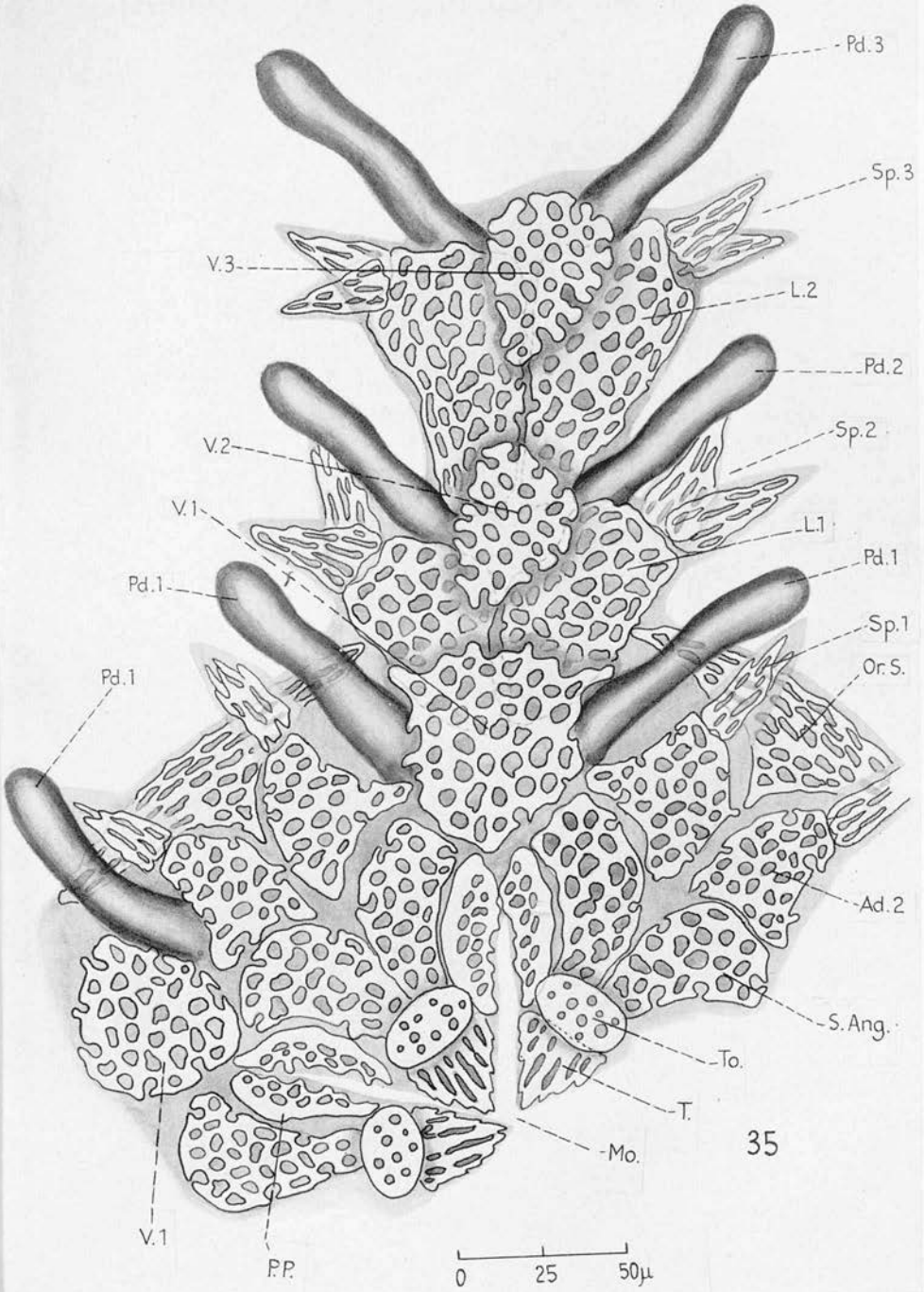
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ECHINODERMS FROM THE SUBANTARCTIC ISLANDS OF NEW ZEALAND: ASTEROIDEA, OPHIUROIDEA, AND ECHINOIDEA

By H. Barraclough Fell, Victoria University College, Wellington

Historical Summary

[*This paper is No. 18 of the "Cape Expedition Series," Scientific Results of the New Zealand Subantarctic Expedition, 1941–45. No. 1 was published in the* New Zealand Journal of Science and Technology, *and Nos. 2 to 15 as Bulletins of the Department of Scientific and Industrial Research.*]

The Subantarctic Islands of New Zealand comprise five groups, all standing upon the New Zealand submarine plateau. They share an echinoderm fauna which presents many resemblances to that of the New Zealand mainland, though possessing distinctive features of its own. At the same time, this fauna is remarkably dissimilar to any other, the most striking distinction, perhaps, being that which separates it from the fauna of nearby Macquarie Island; and the hiatus is more easily understood when it is noted that Macquarie Island does not stand upon the plateau, but is separated from it by deep water. Of the five groups on the plateau, two—namely the Auckland Islands and Campbell Island—were visited by Th. Mortensen in 1914, and as a result of his studies, together with some previous work, notably that of Farquhar (1898) and Benham (1909), the faunal relationships above noted were fairly clear. This paper consolidates and confirms all of Mortensen's conclusions, and supplements them by fresh data from the Snares, and also from the Antipodes groups. The new collections, relatively extensive as compared with former ones, almost double the faunal list, but do not alter our conception as to its external relationships, which are clearly with New Zealand, and with New Zealand alone.

The Snares, lying in latitude 45° S., some 65 miles south of Stewart Island, were discovered by Vancouver in 1791. Till now, our knowledge of their echinoderm fauna has been a record by Farquhar (1898) of a single specimen of an unidentifiable species of *Henricia* collected by A. S. Danby. A collection of starfish made at the Snares by C. A. Fleming in 1947 proves to include four other genera which are now recorded in this paper.

The Bounty Islands, 500 miles east of Stewart Island, in latitude 47° S., were discovered by Bligh in 1798. Although these rocks have been visited on several occasions by naturalists, the only echinoderms so far found are some juvenile specimens of an echinoid and an unidentifiable young ophiuroid, both collected by R. K. Dell, of the Dominion

Museum, in 1950. The echinoid is provisionally referred to *Pseudechinus*, and is recorded in the present paper.

The Antipodes Islands, 490 miles east-south-east of Stewart Island, in latitude 49° S., were discovered by Pendleton in 1800. Yet it was not until 1950—a century and a half later—that the first collection of echinoderms from these remote islets were made by R. K. Dell, of the Dominion Museum. The specimens are referable to three genera, and are recorded here.

Campbell Island lies 330 miles south of Stewart Island in latitude 52° S., and was discovered by Hasselborough in 1810. The first echinoderms were collected by Filhol on the occasion of the visit of the Transit of Venus Expedition in 1874. In 1885 he recorded *Cribrella ornata* (since shown to be *Henricia lukinsii*) and "*Ophidiaster campbelli*" (a *nomen nudum*). Filhol also collected an ophiuroid which Koehler (1907) described as *Amphiura praefecta*. An echinoid, "*Echinus margaritaceus*" recorded by Filhol, has since been shown by Mortensen to have been *Pseudechinus novae-zelandiae*. Benham (1909) added *Amphipholis squamata*. Mortensen (1921–1925) recorded, in addition to the foregoing, *Amphiura amokurae*, *Amphiura norae*, *Amphioplus basilicus*, and *Calvasterias laevigata*—as well as two holothurians (which are not covered in the present paper). Vallin also collected at Campbell Island in 1924, and his results were recorded by Mortensen (1925), who found no additional species. As a result of the collections made by members of the Cape Expedition, the faunal list (excluding holothurians) now stands as follows: Asteroidea, five species representing three genera; Ophiuroidea, five species representing three genera; and Echinoidea, one species.

The Auckland Islands were discovered by Bristow in 1806, and lie 190 miles south of Stewart Island in latitude 50° S. The first record of an echinoderm is a description by Hutton (1879) of a starfish which he named *Asterias rupicola* var. *laevigata*, since named *Calvasterias laevigata*. Farquhar (1898) reported three further specimens of the species from Carnley Harbour, collected by E. Lukins, and also described *Cribrella lukinsii* (now *Henricia lukinsii*). In 1898, Farquhar, in a separate paper, gave Campbell Island as the locality for these same specimens, but this is an obvious slip of the pen. He also recorded *Cribrella ornata* from Auckland Islands, a species since identified as *Henricia lukinsii*. Benham (1908) added *Asterina fimbriata*, later renamed by Koehler (1911) *Asterina aucklandensis*, as it is distinct from the former. Mortensen (1925) added *Ophiomyxa brevirima*, *Amphiura magellanica*, *A. praefecta*, *Amphioplus basilicus*, *Amphipholis squamata*, *Allostichaster insignis*, as well as eight holothurians. The collections made by members of the Cape Expedition now bring the faunal list to seven Asteroidea representing five genera, eight Ophiuroidea representing six genera, and one echinoid, with the possible addition of a second echinoid genus (some uncertainty relating to a locality label).

In this paper the term "Rossian" is employed to denote the marine province comprising the subantarctic islands of New Zealand other than the Snares. The reasons for excluding the Snares are set out under the comments on distribution (page 108).

SYSTEMATIC ACCOUNT

Class *Asteroidea*

KEY TO THE NEW ZEALAND SUBANTARCTIC GENERA

1. Outline of the body defined by a double series of large marginal plates, arranged in an upper series (superomarginals) and a lower series (inferomarginals)	ASTERODON
Marginal plates inconspicuous	2
2. Aboral surface without pedicellariae or large spines, but covered by a more or less uniform coat of spinules	3
Bearing well-developed pedicellariae and spines	4
3. Outline sub-pentagonal	ASTERINA
Five sub-cylindrical elongate arms radiating from a small central disc	HENRICIA
4. Arms 10 or more in number	5
Arms not exceeding 6 in number	STICHASTER
5. Adambulacral plates each bearing 1 spine. Not fissiparous. Arms normally all similar, 5 in number. The young carried in a cluster round the mouth	CALVASTERIAS
Adambulacral plates each bearing 2 spines. Fissiparous transversely, so that the arms usually are arranged in two sets of unequal size, 3 contiguous large ones and 3 contiguous smaller ones	ALLOSTICHASTER

Order *Phanerozonia* Sladen 1899.

The Rossian representatives belong to the family Odontasteridae Verrill (1899), characterized by their broadly stellate or pentagonal form, the presence of an odd interradial marginal plate in each series, and by the presence of either one or two recurved hyaline spines on each pair of oral plates.

Genus *Asterodon* Perrier 1891.

Comparative study of Odontasterid material from the New Zealand mainland, as well as the Cape Expedition collections, makes it necessary to amend the diagnosis of *Asterodon*.

Koehler (1920), in his revision of the Odontasteridae (or Gnathasteridae, as he terms the family), has pointed out that two broad divisions may be made—forms with two recurved spines to each mouth angle, and those with a single spine. To the former division is relegated *Asterodon* Perrier, and also *Diplodontias* Fisher. All other known genera fall in the second division.

The genotype of *Asterodon* is *A. singularis* (Müll. and Trosch.), a Magellanic species in which the marginal plates decrease regularly in size towards the arm-tip. The single New Zealand species hitherto recognized as referable to the genus *Asterodon* is *A. miliaris* (Gray), the marginal plates of which also decrease in size towards the arm-tip.

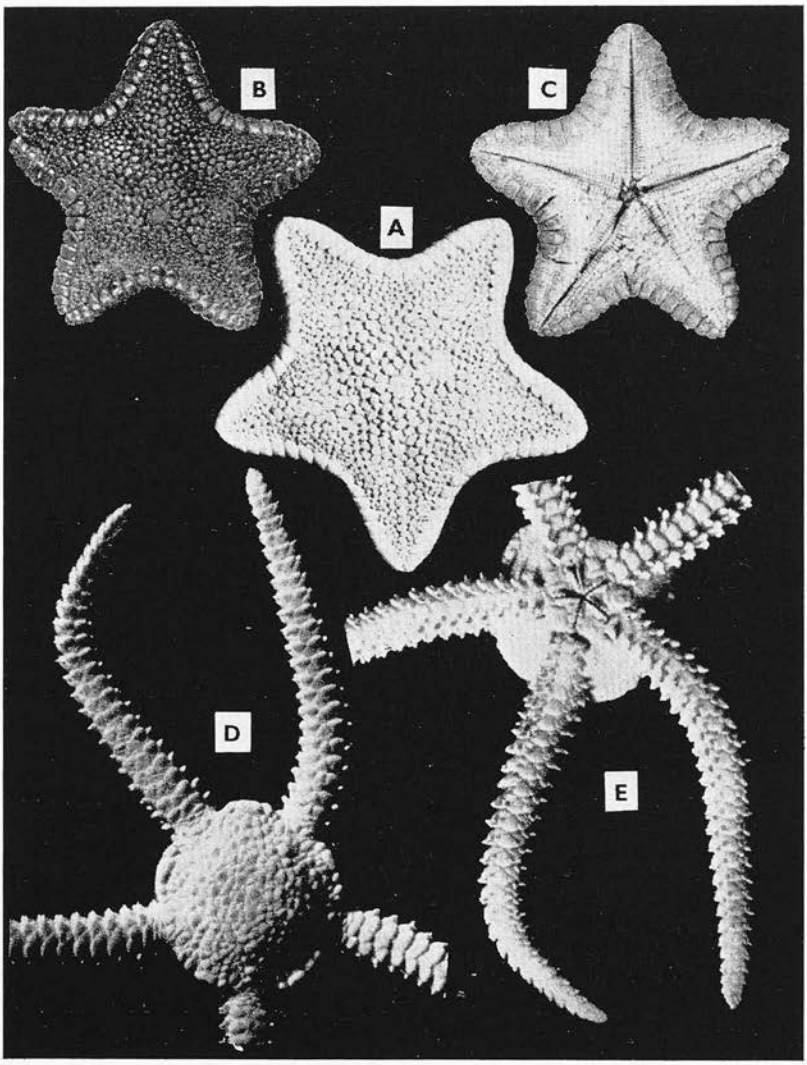

PLATE 1.—A–C, *Asterodon robustus* sp.nov.: A, aboral surface; B, aboral surface denuded of spines, to show plates; C, adoral surface, denuded. D, *Ophioceres marginata* sp.nov., aboral view. E, adoral view.

Perrier in 1894 established a new genus, *Goniodon*, for his species *dilatatus* (previously referred to *Gnathaster*) and gave as the diagnostic feature of the genus the fact that the marginal plates increase in size

at the tip. Fisher (1908) pointed out that the name *Goniodon* is preoccupied by a mollusc, and proposed *Diplodontias* instead. Mortensen (1925) treated *Diplodontias* as a monotypic genus containing only *D. dilatatus*, and drew attention to another feature of the latter species, the possession of glassy warts on the marginal plates. Other distinguishing features of *D. dilatatus* are the large and relatively few marginal plates and the large madreporite.

The Cape Expedition collections from Auckland Island contain a series of specimens representing a new species of *Asterodon*, here described as *A. robustus* (page 80); this species, while agreeing with the diagnosis of *Asterodon*, shows resemblance to *Diplodontias* in respect of the large size of the marginals and their relatively small number. Further, some specimens from both the New Zealand mainland and from the Snares (the latter collected by C. A. Fleming) correspond closely to *Diplodontias dilatatus* in general structure and the possession of glassy warts, but differ in lacking the enlargement of the penultimate marginals. Again, other specimens suggest that the young *Diplodontias dilatatus* does not have the penultimate marginals enlarged, this condition appearing towards maturity. Mortensen (1925) has already shown that the shape of the arm in *D. dilatatus* is very variable, the arms ranging from spatulate forms with broad, rounded tips, to forms which are tapering. Faced with such overlaps between the characters supposed to separate the two genera, *Asterodon* and *Diplodontias*, it appears obvious that two distinct genera can no longer be maintained. *Asterodon* has priority, and to this genus all known diplacanthid *Odontasteridae* should be referred. The revised diagnosis will read:

Genus *Asterodon*.

Odontasteridae possessing two recurved, hyaline spines at each mouth angle, one to each oral plate (Fig. 1, B and C).

Since only three species occur in the New Zealand region, and two of them are subantarctic, a key to all three may be given here.

KEY TO THE NEW ZEALAND SPECIES OF *ASTERODON*

1. Thirty or more marginals to the interbrachial arc (i.e., from arm-tip to arm-tip .... *miliaris*
   About twenty marginals to the interbrachial arc 2
2. Marginals massive, without glassy warts .... *robustus*
   Marginals with glassy warts, the penultimate marginals sometimes enlarged in the adult .... *dilatatus*

Juvenile forms, of course, will show relatively fewer marginals, according to age; in *miliaris*, immature specimens may have only about twenty, whilst in the other two species the corresponding stage may have as few as eleven.

Asterodon dilatatus (E. Perrier)

(Plate 2, A and B)

Synonymy:

Astrogonium miliare Hutton (1872).
Pentogonaster dilatatus E. Perrier (1875).
Guathaster dilatatus Sladen (1889); Farquhar (1898),

Goniodon dilatatus E. Perrier (1894); de Loriol (1901); Farquhar (1907).
Diplodontias dilatatus Fisher (1908); Mortensen (1925).
Goniodon angustus Koehler (1911).

Localities:

Snares Islands.

North-east coast; intertidal, rock shores, under boulders and in crevices; Nov.-Dec., 1947; coll. C. A. Fleming; three specimens.

This is the most southern record of the species, which hitherto has been known only from Cook Strait and the northern part of the South Island. Including material collected at Island Bay (H.B.F. and V. Taylor), from Whekenui Bay, Tory Channel (W. H. Dawbin), and from off Cape Campbell, 50 fathoms (F. Abernethy), there is now available a series of stages in growth of this hitherto little-known species. It is clear that the enlargement of the penultimate marginals does not occur until the disc has begun to exceed 35 mm. major radius, and up to that size specimens have the typical form of *Asterodon*. A tabular summary of the available growth stages follows:

TABLE 1.—Growth Stages and Variation in *Asterodon dilatatus*.

Specimen	Locality	R	r	R/r	No. of marginals in interbrachial arc	Whether penultimate marginals enlarged
A	Cape Campbell	9·0	6·0	1·5	11	No
B	Island B.	17·0	11·0	1·5	15	No
C	Snares	12·0	7·0	1·7	15	No
D	Snares	27·0	16·0	1·7	17	No
E	Snares	27·0	17·0	1·6	19	No
F	Island B.	35·0	18·0	1·9	19	No
G	Tory Channel	45·0	23·0	1·9	23	Slightly so
H	Island B.	50·0	26·0	1·9	21	Yes
I	Tory Channel	50·0	24·0	2·0	23	Slightly so
J	Island B.	53·0	29·0	1·8	19	Yes
K	Island B.	66·0	38·0	1·7	23	Yes

It will be noted that the specimens from the Snares are much smaller than adults from the Cook Strait area. As the former specimens are dried, it is uncertain whether they are immature or represent a smaller southern race.

The ratio of major to minor radii, which ranges from 1·5 to 1·9, evidently varies for any given stage of development, though the larger specimens tend to have the higher ratio. The glassy warts appear early in development, being quite well developed in the smallest specimen of only 9·0 mmR. Though more abundant on the outer marginals, they occur also in some specimens on all the marginals, but tend to be restricted to the inner borders of the marginals towards the interradius.

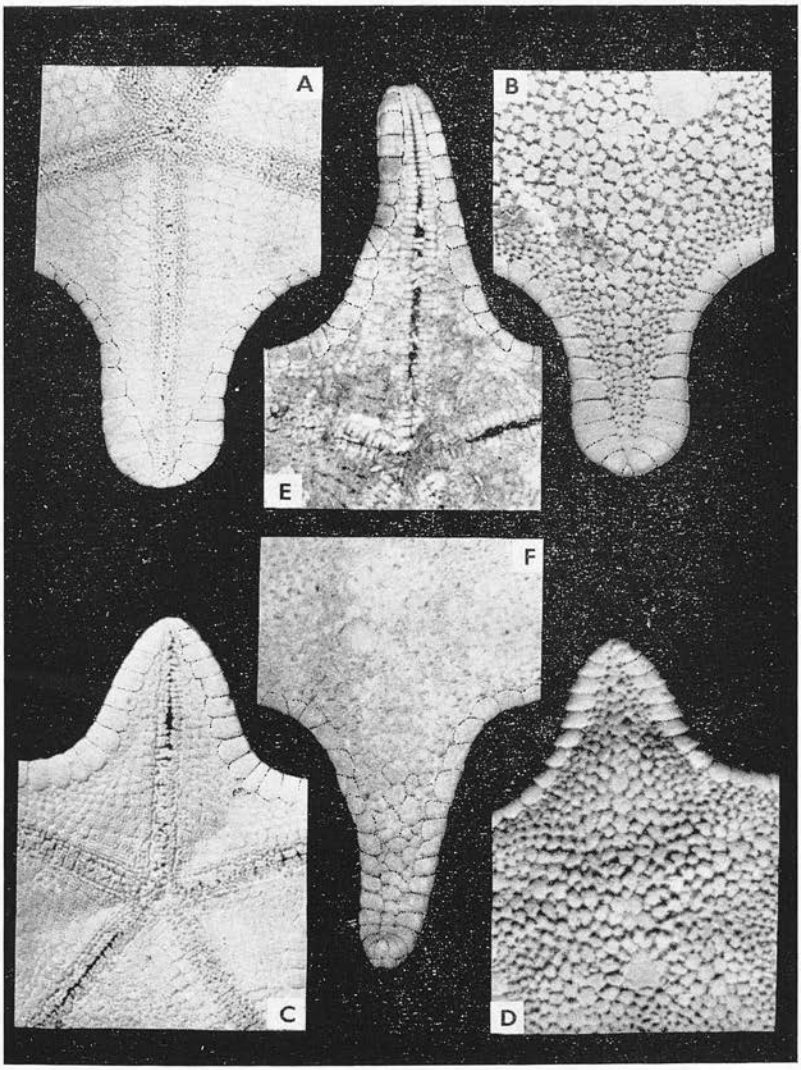

PLATE 2.—New Zealand species of *Asterodon* to illustrate diagnostic features shown by general form and the number and shape of marginals. A, adoral surface of *Asterodon dilatatus*; B, aboral surface of same; C, adoral surface of *A. robustus* sp.nov.; D, aboral surface of same; E, adoral surface of *A. miliaris*; F, aboral surface of same.

Meristic Variation

No meristic variants have been collected, nor is there any record of such in the literature. On specimen D, from the Snares, an abnormality of one radius is present, involving several of the marginals of one side. The fifth marginal from the arm-tip in each series has fused, so that there is only one large marginal at that point, extending from the aboral to the adoral side of the arm. This has caused the neighbouring marginals, especially of the upper series, to assume an irregular form so as to accommodate the sides of the single large compound marginal, which has concave sides.

Colour

At all stages of development this asteroid is strikingly coloured, though in dried specimens the coloration soon fades. The young specimen A was brought in alive by Mr. Abernethy, when the following were noted: The marginals of the upper series are bright orange, the fasciolar divisions between them being buff. The paxillar region above is buff, while the granules of the paxillar plates are orange. The adoral surface is almost uniformly cream, only the outer borders of the lower marginals being tinted orange. The larger specimens assume a less contrasting pattern, the aboral surface becoming a pinkish-buff, and the adoral interradii a creamy-buff. The following data were obtained by tristimulus reflectometry:—

		Aboral surface	Adoral interradius
Spectral equivalent		586 m.mu	579 m.mu
I.C.I. specification	Y	29%	40%
	x	0·3733	0·3634
	y	0·3535	0·3633
Maunsell notation	Hue	6·2YR	2·25Y
	Value	5·81/	6·78/
	Chroma	3·32	3·05

Note.—The figures for Y and Value are probably excessive, as the only specimens large enough for reflectometry were rather faded.

Asterodon robustus sp. nov.

(Fig. 1, A–E; Plate 1, A–C; Plate 2, C and D)

Diagnosis

Form.—Pentagonal, interradii concave, the arms tapering to a blunt tip. R/r, 1·35 to 1·9; mean for 12 specimens, 1·5. Flattened both aborally and adorally. Height up to 0·25 R., but falling to half this value at the arm-tip.

Aboral surface.—Aboral skeleton of closely-packed polygonal plates, arranged as follows (Plate 1 B): A sub-pentagonal, robust, flattened plate in the centre of the disc is surrounded by five radially placed, polygonal, flattened plates of similar size. Distally to the radial plates are five smaller interradial plates. From each radial a row of prominent, flattened, polygonal carinals extends to the arm-tip, becoming smaller towards the distal extremity. The most distal carinal is not contiguous

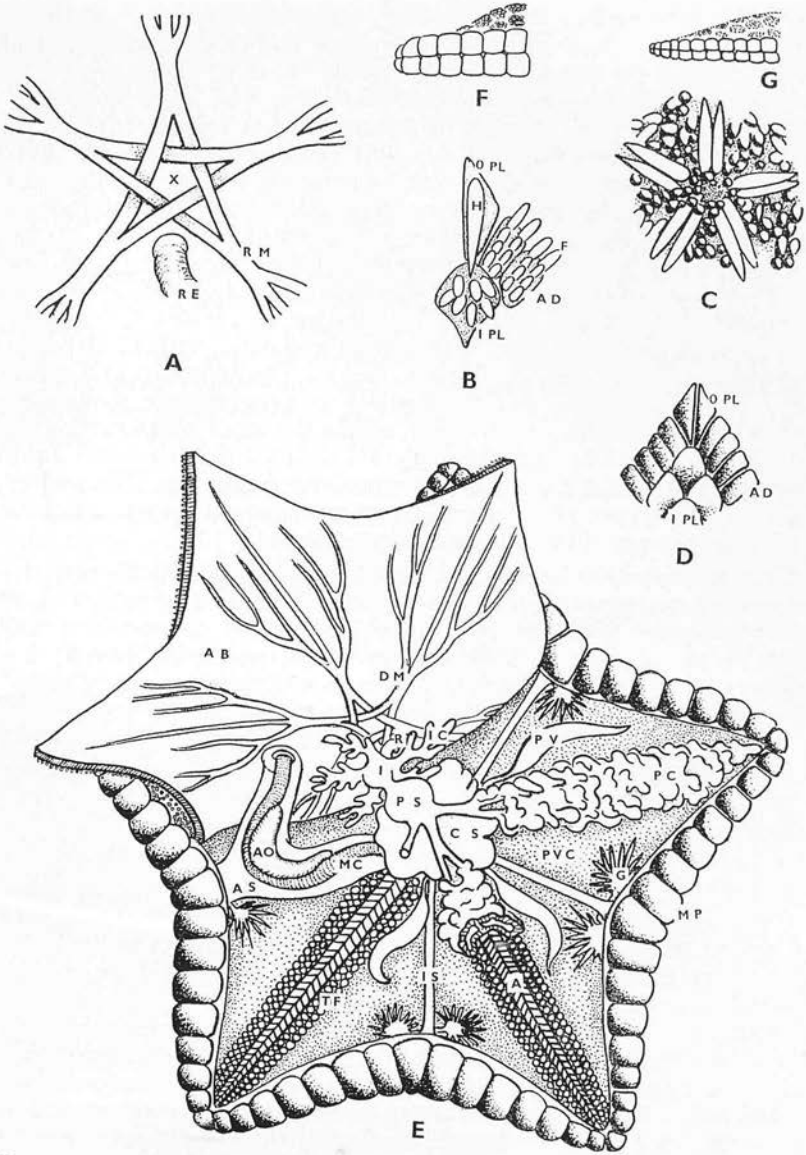

FIG. 1.—*Asterodon robustus* sp.nov.: A, aboral musculature in the apical region; B, detail of the oral skeleton; C, diplacanthid hyaline spines around mouth; D, skeleton of oral region after removal of spinulation; E, general anatomy, part of the aboral body-wall having been reflected; F and G, lateral views of the distal half of the arm in *A. robustus* (F) and in *A. miliaris* (G), both from specimens of ca. 50 mm. major radius, and both to the same scale. Abbreviations: A, ambulacrum; AB, aboral body-wall; AD, adambulacral plate; AO, axial organ; AS, axial sinus; CS, cardiac stomach; DM, radial muscle; F, furrow-spine; G, gonad; H, hyaline spine of oral plate; I, intestine; IC, intestinal caecum; IPL, interradial plate; IS, interradial septum; MC, madreporic canal; MP, marginal (superomarginal) plate; OPL, oral plate; PC, pyloric caecum; PS, pyloric stomach; PV, polian vesicle; PVC, perivisceral coelum; R, RE, rectum; RM, radial muscle; TF, tube-foot ampullae; X, apical area.

with the terminal plate of the arm, from which latter plate it is distinctly separated by the distalmost superomarginals, the latter meeting in the radial midline. On either side of the carinal series of plates lies a row of smaller flattened, polygonal plates, alternating more or less regularly with the median series. Outside these, another, less regular, row can be discerned, or traces of such a row; the remainder of the interradial areas is in each case made up of rather irregularly arranged, contiguous, polygonal plates, becoming successively smaller towards the outer margin against the superomarginals. The upper surface of all the aboral plates is ornamented by irregular, shallow pits and ridges, but no glassy warts occur. The aboral plates are covered by a dense coat of granules, each granule polygonal in outline as viewed from above (owing to close contact with neighbouring granules), each ca. 0·5 mm. horizontal diameter, and ca. 0·5 mm. height. The largest aboral plates carry ca. 40 granules, and the number is progressively diminished towards the interradial distal region, where the small plates carry only 7 to 15 granules. The lateral borders of the aboral plates are free from granules, so that the polygonal outlines of the former are indicated by the mesh of crevices showing on the upper surface of a specimen from which the granules have not been removed.

The madreporite is large (up to 8 mm. diameter), flattened, polygonal in outline, and sculptured by a system of radial furrows and ridges, which sometimes bifurcate. It is situated in one interradius at ca. one-third of the distance from the centre to the interradial margin. Its surface may be slightly sunken below the level of the surrounding aboral plates, or flush with the granular coating of the latter.

The papular pores are situated in clusters of 2 to 6, mainly at the interspaces between the blunt angles of the polygonal aboral plates; a few, however, are found along the lateral interspaces between neighbouring plates, where the latter happen not to be contiguous. They are found all over the upper surface, and as far out as the arm-tips, within the distalmost pair of superomarginals.

The superomarginal plates are massive, much broader than long, and as high as they are broad, forming a most striking border to the body. The unpaired, interradial superomarginal is bluntly cuneiform, having a rounded proximal base, straight sides, and a blunt distal angle. On either side of it extends a row of sub-rectangular superomarginals, gradually decreasing in size towards the arm-tip. The distalmost pair are markedly smaller than the others, and, as already mentioned, are contiguous in the radial midline. The terminal plate is very small, and lies immediately above, and contiguous with, the distal termination of the ambulacral groove. The superomarginals have straight, transverse borders, and are separated from neighbouring superomarginals by deep furrows, but the latter are indistinct until the granular coating is removed, as granules occur on the lateral borders of all of these plates. The granules resemble those of the paxillar area, and are similarly densely arranged, about 150 occurring on the larger superomarginals. The superomarginals are pitted like the aboral plates, and, like them, do not carry glassy warts. A common malformation of these plates is occasionally seen, involving two neighbouring superomarginals; one of them develops as a wedge with a distal base and a proximal angle,

and its neighbour develops as a reversed wedge, with a proximal base and a distal angle—the two fitting together to shape a more or less rectangular or squarish configuration occupying much the same space as would have been the case had no malformation occurred. A similar malformation is found in other species of *Asterodon*, but is especially prominent in *A. robustus* on account of the large size of the marginals involved.

Adoral surface.—The inferomarginals correspond with the superomarginals in regard to all important details, number, position, shape, size, and granulation. (The number of marginals is discussed separately below.) Where a malformation of marginals occurs, either in the upper or lower series, it is not necessarily matched in the other series at the same part of the arm. As a rule, the two distalmost pairs of inferomarginals are at their inner border contiguous with the adambulacral plates of the ambulacral groove. The others are in contact with the outermost of the adoral interradial plates.

The mouth is small and bounded by the prominent oral plates and the spines of the proximal adambulacral plates. It seems that the rigid armature by which it is surrounded would prevent the animal from ingesting objects more than 3 to 4 mm. across. The oral plates are massive (Fig. 1, B, C, and D), each in the form of an isosceles triangle, the base of which is longer than either of the other two sides. The base of the triangle is situated along the interradial axis, and thus adpressed (but not fused) to the base of the triangle formed by the other oral plate of the pair. The two oral plates thus combine to form a diamond-shaped structure at the mouth-angle. Each oral plate carries a prominent recurved spine, attached by its base at the proximal end of the interradial border of the plate, and lying horizontally along the interradial border, with a hyaline tip directed distally. The spines of each pair of oral plates are thus contiguous along the interradial midline. They measure up to 3 mm. in length in an adult specimen, and have the distal portion tapering to a sharp point. The arrangement is thus essentially like that seen in *A. dilatatus* (to which species, in fact, the whole adoral surface of *A. robustus* bears a strong resemblance, as may be seen by comparing Figs. A and C of Plate 2).

The ambulacral groove is narrow (ca. 2 mm. across in an adult specimen) and is about twice as deep as it is wide. It is roofed by a well-developed series of ambulacral plates, opposite each pair of which occurs a corresponding pair of adambulacral plates. Both ambulacrals and adambulacrals decrease in size very gradually towards the arm-tip. Each adambulacral plate carries on its adoral surface several pairs of blunt spines, of which the furrow series is the largest, and the series towards the interradial area the smallest. Each plate bears 4 pairs of such spines in the more proximal region of the groove, but the more distal plates bear only three pairs. The arrangement is thus like that of *A. miliaris*.

The adoral interradial plates (Fig. 1, D; Plate 1, C) are arranged in a manner similar to that of the aboral plates, with the difference that they are all imbricated. In each plate the proximal border is the free

one which overlaps the more deep-seated distal border of the plate lying farther in towards the centre. There are about three series on each side of the adambulacral plates, running parallel with the latter, but larger and less numerous than the adambulacrals. The interradials alternate in the usual manner and decrease in size distally. Towards the interradial margin they become much smaller and are irregularly arranged, though still imbricating. Each plate is sculptured by a number of circular pits which correspond in number and position to the granules which it bears. The larger plates carry ca. 20 granules, similar to those of the aboral plates, and the outer plates carry fewer. In the more proximal part of the interradial area, the boundaries of the interradial plates are faintly indicated by divisions between the groups of granules, but the distal part of the area is so crowded with granules that the outlines of the plates cannot be distinguished until the granules are removed.

Type.—The holotype and syntypes are deposited in the Dominion Museum.

The specific name proposed refers to the massive character of the skeletal plates.

Localities

Lord Auckland Group:

Mainland (Bristow Island):

Tagua Bay, Carnley Harbour, on rocks with *Calvasterias*, 12/10/43; coll. W. H. Dawbin, 1 spec.

Deas Head, Port Ross, 1942; coll. C. A. Fleming, 2 specimens.

Opposite Passage Inlet, in shallow shell-bottom pools, 24/8/43; coll. R. W. Balham and W. H. Dawbin, 3 specimens.

Kekeno Bay, among *Xiphophora* bases on sheltered boulders, 12/9/43; coll. W. H. Dawbin, 3 specimens.

Enderby Island:

East coast, cast up on shelly beach; coll. W. H. Dawbin, 1 spec.

Passage Islet:

Coll. R. A. Falla, 2 specimens.

Growth and Variation

In the material on hand, the average number of marginals in each series, over one complete interbrachial arc, is 17; the extreme values noted are 13 and 19 respectively. The number of marginals, as is usual, increases with age, but the increase is relatively very slight in this species, and equivalent to a rate of 1 additional marginal pair in each series to every 7 mm. growth of R. Variation in the value of the ratio R/r is not correlated with age. The following tabular survey of all

available material gives some indication of the range of variation occurring in this asteroid:—

TABLE 2.—Growth Stages and variation in *Asterodon robustus*.

Specimen	Locality	R mm.	r mm.	R/r	No.of marginals in interbrachial area
A	Kekeno Bay	35	26	1·35	13
B	Opposite Passage Island	35	26	1·35	15
C	Opposite Passage Island	39	25	1·56	15
D	Passage Island	49	34	1·44	17
E	Opposite Passage Island	52	34	1·53	15
F	Kekeno Bay	52	37	1·41	17
G	Enderby Island	53	28	1·90	13–15
H	Kekeno Bay	58	33	1·76	17–19
I	Tagua Bay	59	40	1·48	17
J	Deas Head	60	38	1·58	15–17
K	Deas Head	64	42	1·52	19
L	Passage Island	67	44	1·52	19

Meristic Variation

There are no meristic variants in the collection.

Colour

Dr. R. A. Falla has kindly lent a water-colour sketch of the aboral aspect, made at Port Ross, and Mr. W. H. Dawbin has also supplied notes made from life. The whole aboral surface is a uniform, rich, chocolate-red, and this colour extends over the marginals to include, on the adoral side, the inferomarginals and the outer border of the adoral interradial areas. The peristomial region is a lighter orange-yellow tint, which becomes gradually darker as one passes distally towards the margin. The following measurements were taken by tristimulus filters on a dried specimen which had retained fairly closely the original colour:—

Aboral surface:

Spectral equivalent .... 590 m.mu

I.C.I. specification .... Y 5%
x 0·3622
y 0·3282

Munsell notation .... Hue 2·25 YR
Value 2·1/
Chroma 1·3

Adoral surface, interradial mid-area:

Spectral equivalent	583 m.mu
I.C.I. specification	Y 17% x 0·3932 y 0·3815
Munsell notation	Hue 10 YR Value 4·68/ Chroma 3·34

Breeding Habits

Nothing is known. One specimen which was dissected had unripe gonads; it had been collected in August. It may therefore be tentatively assumed that breeding will occur in the summer or autumn. The collection does not include any formalin material collected in the latter seasons.

General Anatomy

Some of the more interesting features of the internal anatomy may be noted here (see Fig. 1, E).

Owing to the relatively great thickness of the skeletal plates, the perivisceral coelum is reduced to a shallow, star-shaped space within which the internal organs are crowded together. Despite the large skeletal plates, the muscular system is remarkably undeveloped. The aboral musculature comprises only a slender dorsal perradial muscle along each radius, giving off on either side a lateral (adradial) branch from near the proximal end. Each lateral branch divides dendritically several times. Each perradial muscle bifurcates at its proximal extremity, and the two halves cross the interradii around the central region of the disc so as to form a peculiar interlaced ring in conjunction with the bifurcations of the other five perradial muscles. In the asteroid *Pentaceros reticulatus*, a somewhat similar system has been figured by Tennent and Keiller (1911), but these authors do not refer to any central ring formation in the latter species.

The cardiac stomach is rather small and evidently not capable of very great eversion. The pyloric stomach is small and spherical, and receives the ducts of the pyloric caeca, which latter organs do not present any peculiarity. The intestine is provided with five short, branched intestinal caeca. It is interesting to note that the rectum does not traverse the centre of the muscle ring, but reaches the aboral surface by passing to one side of the latter, in an interradius.

The gonads are paired in each interradius, separated from each other by a prominent interradial septum. They lie closely approximated to the inferomarginal plates. In the specimens examined, the gonads were too small to determine with certainty the sex, nor were the gonoducts clearly distinguishable; the latter probably open near the interradial septum, on the adoral surface.

The stone-canal is strongly flexed, and surrounded by the axial sinus. Its walls are heavily calcified, and marked by transverse rings, simulating a trachea. A large elliptical axial organ lies against the inner curve of the flexure. A large, elongate polian vesicle lies in each interradius, on the adoral floor, on either one side or the other of the interradial

septum; there seemed to be no regularity governing the precise location of the vesicle in each case.

Order *Spinulosa* Perrier

There are only two genera of Spinulosa known from the Rossian province, *Asterina* (Fam. Asterinidae) and *Henricia* (Fam. Echinasteridae). The two genera may easily be distinguished by their macroscopic appearance as set out in the key on page 75.

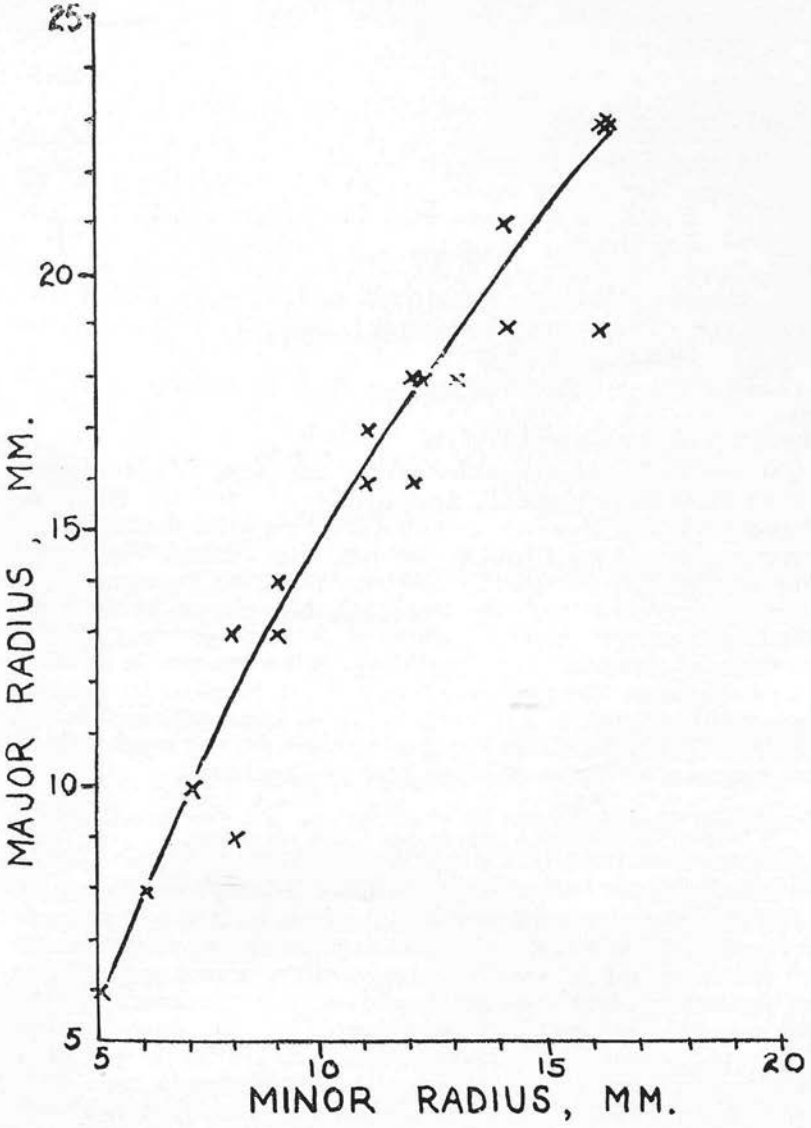

FIG. 2.—*Asterina aucklandensis*: Variation of major and minor radii at different growth stages, based on eighteen individuals.

Genus *Asterina* Nardo 1834

There is only one species, *Asterina aucklandensis*, distinguished from all other New Zealand species by possessing a cluster of about 100 hyaline spinules on each of the numerous, imbricating aboral plates.

Asterina aucklandensis Koehler

Synonymy:

Asterina fimbriata Benham (1909).

Asterina aucklandensis Koehler (1920); Mortensen (1925); Bennett (1927).

Localities:

Lord Auckland Group:

Mainland (Bristow Island)
Tagua Bay, among boulders at low tide, 18/9/43; coll. W. H. Dawbin, 6 specimens. Also May, 1943; coll. D. McNabb, 3 specimens.
Carnley Harbour; coll. D. Knowles and H. Pollock, 1 specimen.
Musgrave Peninsula, littoral; coll. C. A. Fleming, 1942, 3 spec.
Crozier Point, among boulders at low tide, 10/9/43; coll. R. W. Balham, 4 specimens.

Campbell Island: coll. J. H. Sorensen, 1943; 1 specimen.

Previously Known Localities

The species has been recorded earlier only from Masked Island, Carnley Harbour, in the Lord Auckland Group (Benham, 1909; and Mortensen, 1925). However, Bennett (1927) recorded doubtfully two young specimens from Lyttelton Harbour, New Zealand. These were too young to show the specific characters clearly, but a comparison of Bennett's description with the two smallest specimens in the Cape collection (specimens A and B) shows so close an agreement that the occurrence of the species as far north as Lyttelton can now be regarded as probable rather than possible. It has not been found as far north as Cook Strait, although a close watch for it has been kept over the last three years, when more than 700 specimens of *Asterina regularis* have been examined at Victoria College Zoology Department.

Growth and Variation

Although Mortensen (1925) reports a specimen reaching R 28 mm., the largest example in the Cape collection measures R 23 mm.

The ratio of major to minor radii varies from 1·12 in a young specimen up to 1·62 in a medium-sized one. A meaned curve of the ratio R/r plotted against R (see Fig. 2) suggests the interesting possibility that the shape of *Asterina aucklandensis* is not a simple function of age, as is normally the case. In the young specimens, the shape is nearly pentagonal, the ratio R/r having a value of ca. 1·2. With increase in size, the shape becomes at first more star-like, owing to more rapid growth along R than along r, and the ratio R/r reaches a maximum value of 1·5 (mean) when R is ca. 14 mm. Thereafter growth along r tends to overtake that along R, so that in the largest specimens the

form is again more pentagonal, with a mean value for R/r of 1·4 in specimens larger than 20 mm. A graphical presentation of the data follows (Fig. 3).

Meristic Variation

Insufficient material is available to state the incidence of six-rayed forms, but since two of the eighteen specimens collected are hexamerous, it would seem that they occur more frequently than in *Asterina regularis*, where the incidence in 713 Cook Strait specimens proves to be only 1·8%.

Colour

All the preserved and dried specimens in the Cape collection are bleached to a pale creamy-buff, so no accurate colour data can be presented. Fortunately, however, members of the expedition made

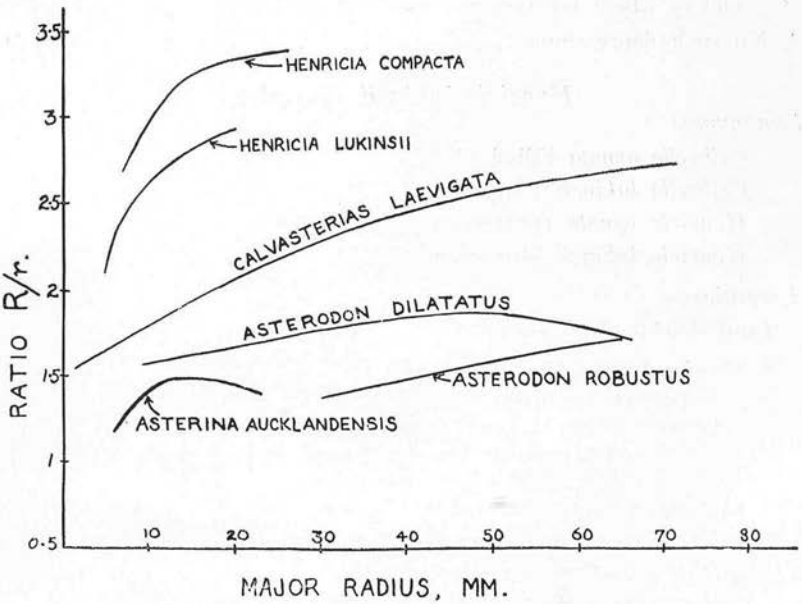

FIG. 3.—Meaned curves for the variation of the ratio major/minor radius against major radius in six species of asteroids. Further details in text.

careful notes from life. Apparently some colour variation occurs. A watercolour sketch by Dr. R. A. Falla shows the aboral surface orange, suffused with a purplish-brown counter tint, save at the ambitus, which is a purer orange. A similar colouring is noted by Mr. W. H. Dawbin. Mr. D. McNabb records specimens as purple-brown above, underside white. Benham (1909) recorded "orange-red or reddish-brown," while Mortensen (1925) reported a "beautiful claret colour."

Breeding Habits

Mortensen (1925) has found that the eggs are large and yolky, but nothing is known of the development.

General

To judge by the frequency of regenerating or truncated arms, the species is liable to attack by some predator, which apparently removes the distal extremities of the arms. The food of *A. aucklandensis* appears to be mainly detrital.

Genus ***Henricia*** Gray 1840

Characterized by a more or less closely meshed skeleton bearing numerous small spinules either in groups or scattered along the ridges formed by the aboral skeletal plates. Marginal plates very small, but generally distinguishable. Adambulacral plates with one or more spinules placed deeply in the furrow. No pedicellariae.

KEY TO THE ROSSIAN SPECIES OF *HENRICIA*

1. Adoral interradii each with a depression, at the distal end of which the gonopores are situated .... *lukinsii*
2. No such depressions .... *compacta*

Henricia lukinsii (Farquhar)

Synonymy:

Cribrella ornata Filhol (1885).
Cribrella lukinsii Farquhar (1898).
Henricia ornata (partim) Benham (1909).
Henricia lukinsii Mortensen (1925).

Localities:

Lord Auckland Group:

Mainland (Bristow Island):
Musgrave Peninsula, littoral, 1942; C. A. Fleming, 4 specimens.
Crozier Point, 2/3/43; 1 specimen.
North coast, opposite Passage Island, in rock pools; coll. W. H. Dawbin, 24/8/43, 19 specimens.

Enderby Island:
North coast, in rock pools, 19/8/43; coll. E. F. Doley, 10 spec.

Campbell Island:

Windlass Bay, 20/7/44; coll. R. W. Balham, 3 specimens.

Previously Known Localities

The species is endemic to the Rossian province. It has earlier been recorded from Carnley Harbour by Farquhar (1898), Mortensen (1925); from Figure Eight Island by Mortensen (1925); from Masked Island by Benham (1909), Mortensen (1925); from Perseverance Harbour, Campbell Island, by Mortensen (1925).

Growth and Variation

R reaches a maximum of 24 mm., according to measurements given by Benham (1909). The largest Cape specimen measures R 18 mm. The ratio R/r varies from 2·0 in the youngest specimens in the collection (of R 5 to 6 mm.) to a maximum of 3·2 in specimens of

ca. 20 mm. R. The ratio increases with size, and hence in all probability with age, and a meaned curve (Fig. 2) shows that the rate of increase is more rapid in the earlier stages than in the later. The curve also shows that the range of mean value at any point is 0·35. Since these data cover all the significant features and provide a suitable basis for comparison with *Henricia compacta*, there is no need to give a tabulated summary.

Meristic Variation

No variants occur in the collection, and none is recorded in the literature.

Colour

The colour of preserved and dried specimens is fugitive—brown in the latter, buff or white in the case of alcohol or formalin specimens; consequently, no precise specifications can be given. All collectors state, however, that the colour in life is bright orange, while the adoral surface is lighter, according to Mr. D. McNabb.

Breeding Habits

Mortensen (1925) has suggested that the interradial adoral depressions may serve as brooding chambers. Although specimens have been collected in March, May, July, August, November, and December by the various visiting collectors and the Cape Expedition, no evidence of such behaviour has been obtained. However, in *Henricia sanguinolenta*, a brood-protecting species of the North Pacific and North Atlantic, only three weeks are required for the development, so that it is still quite possible that a similar development may occur in *H. lukinsii*, as yet unobserved.

General

The species is commonly found with regenerating arms, and may be subject to predator attack.

Henricia compacta (Sladen)

Synonymy:

Henricia ornata (partim) Benham (1909).

Henricia compacta aucklandiae Mortensen (1925).

Localities:

Campbell Island:

North-west beach, among algae at low tide, 29/10/47; coll. J. H Sorensen, 1 specimen.

Also 3 other specimens, no locality given, 1943; coll. J. H. Sorensen,

Lord Auckland Group:

Mainland (Bristow Island)

Opposite Passage Island, in rock pools, 24/8/43; coll. W. H. Dawbin, 3 specimens.

Tagua Bay; coll. D. McNabb, 3 specimens.

French Island, 16/4/44; coll. E. G. Turbott, 1 young specimen.

Ewing Island

Under boulders at low tide, 28/2/43; coll. W. H. Dawbin, 1 specimen.

From sheltered rock pool, 7/8/43; coll. W. H. Dawbin, 1 spec.

Previously Known Occurrence

Benham (1909) recorded the form from the Auckland Islands only, and Mortensen (1925) also gives only Carnley Harbour, Auckland Islands, but also lists specimens from the Chatham Islands. The record given above for Campbell Island is apparently new. The possibility of this asteroid occurring at the Snares Island must also be considered (see *post*).

Variation

Mortensen (1925) was the first to refer this species to *Henricia compacta*, but considered it of distinct varietal status on account of the "spinelets being less robust and fewer in each group. Also the madreporite is much more distinct in the Auckland form than in my specimens of *compacta*." In the rather more extensive material from the subantarctic islands which is now available, the robustness of the spinelets, as well as the number of them in each group, shows much variation, and I can find no constant difference from material corresponding to *Henricia compacta* collected for me by Mr. F. Abernethy in the Chatham Islands. *H. compacta* is well distinguished by the biserial arrangement of the spinules of the intermediate plates. All the specimens show constancy of these characters. Thus, *H. compacta* ranges from the Chatham Islands to the Rossian province, and there is no subspecies confined to the latter area.

Growth Changes

In comparison with *Henricia lukinsii*, *H. compacta* undergoes during development a relatively more rapid growth along the major radii, so that adult forms have much longer arms than do adults of the former species. R reaches a maximum of 42 mm., according to Benham (1909); but the largest Cape specimen is much smaller, measuring only R 26 mm. The ratio R/r varies from a mean value of 2·7 in young specimens of R 8 mm. to 4·2 in Benham's largest specimen of R 42 mm. As in *Henricia lukinsii*, the ratio increases with size, and a meaned curve (Fig. 2) provides a convenient means of comparison between the two species.

Meristic Variation

No variants are recorded, and none occurs in the collection.

Colour

This is fugitive in preserved or dried material, but fresh material from the Chatham Islands was bright orange above and paler buff or cream below. Mr. D. McNabb records a similar colour for specimens from Tagua Bay, Auckland Islands. A specimen collected by Mr. W. H. Dawbin at Ewing Island is noted as dark grey, and several other specimens in the collection retain some evidence of a greyish tint.

Breeding Habits.

Unknown.

Henricia sp.

Farquhar (1898) records a much distorted specimen of an asteroid collected by Danby, in the Snares Islands, and refers it to *Cribrella ornata* Perrier. As both the above-mentioned species have been referred to *Cribrella ornata*, it is uncertain which species is concerned in this instance. Mr. C. A. Fleming, in 1947, collected echinoderms at the Snares, but did not obtain any species of *Henricia*.

Order ***Forcipulata*** Perrier 1894

Three genera of Forcipulata occur in the Rossian province, all referable to the Family Asteriidae. They are *Stichaster, Allostichaster*, and *Calvasterias* (see key to genera on page 75).

Genus ***Stichaster*** Muell. & Trosch. 1840

The coarse, granuliform spines of the aboral surface—resembling a coating of pin-heads—are characteristic. The single species occurring throughout New Zealand cannot with certainty be distinguished from two specimens obtained from the Snares by Mr. C. A. Fleming.

Stichaster australis (Verrill)

Synonymy:

Coelasterias australis Verrill (1867); Hutton (1872).

Stichaster australis Sladen (1889); Farquhar (1895); Farquhar (1898); Mortensen (1925).

Coelasterias australis Koehler (1920).

Locality:

Snares Island: On algae-covered rocks, intertidal, 27/11/47; coll. C. A. Fleming, 2 specimens.

Remarks

Stichaster australis now becomes numbered among the most eurytopic echinoderms of New Zealand, extending from North Cape to the Snares. The species is already well known from descriptions and figures in the references noted above, so that no details need be listed here. One feature in which both the Snares specimens differ from Cook

Strait examples is that the carinal granular spines are more compactly arranged in the former; also, the disc is more densely covered by spines. Both specimens are smaller than average mainland examples, one having R 80 mm., and the other R ca. 57 mm.

Genus *Allostichaster* Verrill 1914

The single Rossian species may be distinguished by the generic characters given above, with which have been included the specific characters of the Rossian form—namely, the possession of 6 arms in two sets of 3. The only other New Zealand species, *Allostichaster polypax*, which has 8 arms in two sets of 4, is unknown from the Rossian province.

Allostichaster insignis (Farquhar)

Synonymy:

Stichaster insignis Farquhar (1895); Farquhar (1898); Farquhar (1898A); Benham (1909B).

Allostichaster insignis Koehler (1920); Mortensen (1925).

Localities:

Lord Auckland Group:

Mainland (Bristow Island):

Musgrave Peninsula, littoral, 1942; coll. C. A. Fleming, 2 spec.

Laurie Harbour, Port Ross, near Head of Bay, in 10 fathoms, 16/2/43; coll. W. H. Dawbin, 1 spec.

Tagua Bay, under stones at low tide, 30/9/43; coll. W. H. Dawbin, 4 spec.; also on seaweed brought up on anchor-chain, 20/4/47; J. H. Sorensen, 1 spec.

Ranui Cove, Port Ross, in *Macrocystis* holdfast, 19/7/43; coll. W. H. Dawbin, 1 spec.

Snares Islands: North-east coast, on intertidal rocks, November, 1947; coll. C. A. Fleming, 1 spec.

Previously Recorded Occurrence

Mortensen (1925) recorded the species from Masked Island, Figure Eight Island, and Port Ross, in the Aucklands group. It ranges from Cook Strait southward, but is not yet known from the Campbell Islands.

Variation

On account of the fissiparous habit, no certain deductions may be drawn as to growth changes, for small three-rayed individuals may be portions accidentally detached from larger specimens. However, the general absence of any specimens of large size suggests that the species does not reach so large a size in the Rossian area as it does in the Cook Strait region. Specimens from the latter area may reach R 50 mm., whereas the largest known Rossian forms have R 15 mm.

For the purpose of comparison with the typical mainland form, the following tabular summary lists all the Cape material, that from the Snares, and sample Cook Strait specimens:—

TABLE 4.—Variation in *Allostichaster insignis*.

Specimen	Locality	Regenerating portion			"Parental" portion		
		R mm.	r mm.	No. of arms	R mm.	r mm.	No. of arms
A	Auckland Islands	2·5	1	3	5	2	3
B	Auckland Islands	–	–	–	6	2·5	3
C	Auckland Islands	–	–	–	7	3	3
D	Auckland Islands	–	–	–	7	3	3
E	Auckland Islands	–	–	–	8	3·5	6
F	Auckland Islands	4	2·5	3	9	4	3
G	Snares	8	3	3	12	3·5	3
H	Auckland Islands	6	2·5	3	14	4	3
I	Auckland Islands	8	3	3	15	4·5	3
J	Cook Strait	–	–	–	17	4	3
K	Cook Strait	2	?	3	17	4	3
L	Cook Strait	–	–	–	19	4	3
M	Cook Strait	–	–	–	34	9	6

The number of madreporites is also variable. Larger specimens with 6 rays generally possess 4 separate madreporites, and this number is presumably characteristic of the adult. However, 3-rayed specimens may have either 1 or 2 madreporites. One specimen, not listed in Table 4, has arms of three distinct sizes: 2 arms of R 7 mm., 3 arms of R 3·5 mm., 1 arm of R 1·5 mm. Specimen M, a large 6-rayed specimen, shows no sign of ever having divided, so that apparently fissiparity may be considerably delayed in some cases. The whole question is, however, too involved for discussion here; it is evident that life-history studies should be made of this peculiar species, which is common enough for intensive investigation.

Genus *Calvasterias* Perrier 1875

There are two Rossian species, distinguishable by the key which follows, save in the case of a few individuals, usually young ones, where the diagnostic features are not always clearly exhibited.

KEY TO THE ROSSIAN SPECIES OF *CALVASTERIAS*

1. A well-marked carinal series of spinelets on each arm, the spinelets in transverse arcs, or clusters of 3 or 4, along most of the carinal series .... *C. suteri*
2. No aboral spines, or merely irregularly scattered spinelets, or if a carinal series is present it is monoserial, lacking transverse arcs or clusters .... *C. laevigata*

Calvasterias laevigata (Hutton)

Synonymy:

Asterias rupicola var. *laevigatus* Hutton (1879).
Stichaster Suteri var. *laevigatus* Farquhar (1898); Benham (1909).
Calvasterias laevigata Fisher (1923); Mortensen (1925).

Localities:

Campbell Island:

Tucker Cove, under stones in tidal zone, 5 small specimens, some with clusters of young attached to the lower surface around the mouth; coll. J. H. Sorensen, 4/11/47. Dark green in life fading in alcohol to cream).

Venus Bay, under stones at low-tide mark, 5 specimens, some with clusters of young; coll. J. H. Sorensen, 28/11/47.

West coast, under rocks in tidal pools, 21 specimens, all immature; coll. J. H. Sorensen, 20/2/47.

North-west bay, 2 specimens; coll. R. A. Falla, 26/8/43.

Venus Bay, tidal zone, 5 specimens; coll. J. H. Sorensen, 23/8/43.

Shoal Point, from rock-pool at low tide, 2 specimens; coll. J. H. Sorensen, 5/3/46.

Antipodes Islands:

Ringdove Bay, in low-tidal pools and crevices, 6 immature specimens without young; coll. R. K. Dell, November, 1950.

Lord Auckland Group:

Mainland (Bristow Island)

Crozier Point, 18/8/43, 10/9/43, among sheltered boulders, low tide; coll. W. H. Dawbin, J. Jones, R. W. Balham; 27 specimens, some with broods.

Tagua Bay, D. McNabb, May, 1943; 19 specimens, some with eggs, no broods.

Crozier Point, 8/8/43, 13 specimens; coll. W. H. Dawbin.

Tandy Inlet, 4 specimens, one with a partly-ingested isopod protruding from the mouth; coll. W. T. Wenham, 1945.

Tagua Bay, under rocks, at low tide, with brood; coll. W. H. Dawbin, 28/11/43, 2 specimens.

Crozier Point, among boulders at low tide, with brood, 5 specimens; coll. J. Jones, 11/9/43.

Crozier Point, under partly sheltered boulders, with brood, 37 specimens; coll. W. H. Dawbin, 8/8/43.

Tagua Bay, intertidal, 4 specimens; coll. E. G. Turbott, November, 1944.

Camp Cove, Carnley Harbour, intertidal, 3 specimens; coll. E. G. Turbott, 26/10/44.

Crozier Point, under sheltered boulders at low tide, with young, 6 specimens; coll. W. H. Dawbin, 18/8/43.

Tagua Bay, 1 specimen, coll. M. G. Easton and E. G. Turbott, 21/8/44; 1 specimen under stones at low-tide level, coll. W. H. Dawbin, 30/943; 5 specimens on rocks at low-tide level, coll. W. H. Dawbin, 22/10/43.

Auckland Island, 1 specimen, E. G. Turbott, 1944.

Opposite Passage Island, in channel, on *Mytilus magellanicus* beds (with *C. suteri*), 19 specimens; coll. W. H. Dawbin, 24/8/43.

Masked Island, under stones, low tide, 2 specimens, 2/5/43.

French Island, on rock ledges, with brood, 1 specimen, 26/8/43.

Remarks

Calvasterias laevigata, which is unknown from the New Zealand mainland, proves to be the commonest echinoderm of the subantarctic islands of New Zealand, occurring at the Antipodes, the Lord Auckland, and the Campbell Islands at most seasons, and being represented in the combined collections by almost 200 specimens. Outside the Rossian area, it is unknown, nor is it known from the Snares, a fact which tends to stress the essentially mainland character of the echinoderm fauna of the latter islets.

Colour notes made by W. H. Dawbin and other collectors show a variation from dark grey, or dark green, to yellow ochre or light fawn, tending to be darker towards the centre of the animal, or a rich brown. All small specimens were dark grey or green, but the very young individuals from a brood still clinging to the parent are bright orange. Dawbin (private communication) noted specimens with the stomach everted around an isopod, a chiton, gasteropods, and *Halicarcinus planatus*.

The relative wealth of material prompts some observations on growth changes. As may be seen from an analysis of 159 specimens (Fig. 4), the maximum size reached is about 7·7 cm. major radius, the mode for the sample occurring at R 2·5 cm. Sexual maturity (as judged by the presence of a brood) is reached at R 1·5 cm., so that 75% of the sample was mature. Both 6-rayed and 4-rayed forms occurred, but the incidence of either was less than 1%. A study of the variation of form with size (Fig. 3) gives a mean curve for the ratio R/r against R, from which all points save one did not diverge more than about ± 0·4 (for the value R/r). The slope of the mean indicates a tendency through life for the arms to grow relatively faster than the interradial region, the tendency gradually falling off towards the maximum value of R.

It appears that eggs are laid in early winter (May). Broods are carried through a considerable part of the year, having been taken in August, September, October, November, and also April. The latter case (from Campbell Island) comprised relatively advanced young of ca. 2·5 mm. across, and so must have been a carry-over from the previous breeding. But it seems, from the general absence of broods

from specimens taken in the late summer and early autumn, that the young must become free-living, usually in the mid-summer. The protection of the eggs may possibly be connected with the rather unusual habit of breeding in the severest months of the year. The presence of the cluster of young over the entire oral region would seem to preclude the possibility of the parent's feeding, for the young remain in a dense cluster, even when placed in preservative, thus making it seem unlikely that they would leave the parent to enable it to feed from time to time.

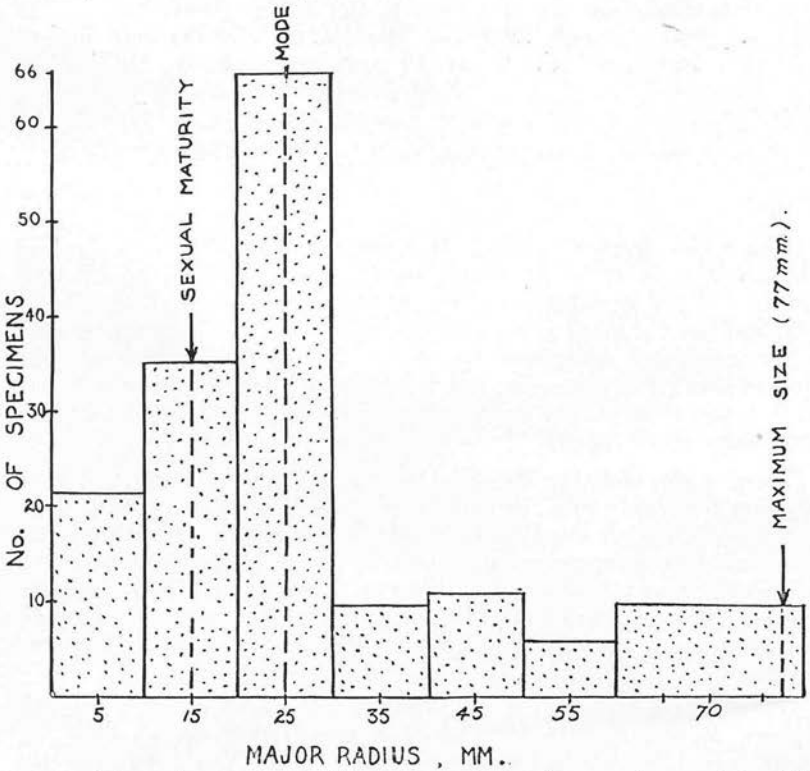

FIG. 4.—*Calvasterias laevigata*: Histogram analysis of a sample comprising 159 individuals, to show the incidence of specimens in seven graded size categories. Further details in text.

Calvasterias suteri (de Loriol)

Synonymy:

Asterias rupicola Hutton (1878).

Stichaster suteri De Loriol (1894); Farquhar (1897); Benham (1909).

Stichaster littoralis Farquhar (1895).

Stichorella suteri Koehler (1920).

Calvasterias suteri Fisher (1922); Mortensen (1925); Bennett

Localities:

Snares Islands:

Intertidal, rocky north-east coast, 2 specimens; coll. C. A. Fleming, November, 1947.

Campbell Island:

Windlass Bay, 2 specimens; coll. R. W. Balham, 20/7/44.

Under rocks, in tidal pools, west coast, 1 specimen; coll. J. H. Sorensen, 20/2/47.

Lord Auckland Group:

Mainland (Bristow Island)
28/11/43.

Opposite Passage Island, on *Mytilus magellanicus* bed in Passage, 4 specimens; coll. W. H. Dawbin, 24/8/43.

Tagua Bay, among boulders, low tide, 2 specimens; coll. W. H. Dawbin, 18/9/43.

Ranui Cove, 2 specimens; coll. E. G. Turbott, February, 1944.

Shores of Musgrove Peninsula, littoral, 2 specimens; coll. C. A. Fleming, 1942.

Carnley Harbour, probably dredgings, 6 specimens; coll. C. A. Fleming, 1942.

Ewing Island

Under boulders, mid-tide, 4 specimens; coll. W. H. Dawbin,

Antipodes Island

Ringdove Bay, in low-tidal pools and crevices, 2 very young specimens (R 7 mm. and 3·5 mm.) show an incipient spine-formation resembling *C. suteri*, but perhaps a young phase of *C. laevigata* (of which latter species 6 specimens were taken at the same time); coll. R. K. Dell, November, 1950.

Remarks

Calvasterias suteri occurs on the New Zealand mainland, where Bennett (1927) found specimens with young broods in October. No information as to its breeding habits in the subantarctic is available other than the fact, noted whilst dissecting a Campbell Island specimen, that immature ova were developing in the gonad in February. The following supplementary colour notes may be added to Bennett's account: some specimens from Bristow Island are recorded as having been light fawn or fawn-brown, darker in the centre; others, from the same locality, were grey-green, with white spines, the animal appearing almost black when viewed in the sea from above; at Tagua Bay, some fawn and some grey specimens were seen. These colour notes were made by W. H. Dawbin.

Class: *Ophiuroidea*

KEY TO THE ROSSIAN GENERA OF OPHIUROIDEA

1.	Disc and arms covered by soft dermis	OPHIOMYXA
	Disc and arms covered by calcareous plates	2
2.	Disc covered by a closely-set granulation, which obscures the calcareous plates, save on the arms, where the plates are very distinct	PECTINURA
	No granulation on disc	3

3. A single upper arm-plate to each arm-segment, and a single lateral arm-plate on either side of the segment 4

Upper and lateral arm-plates are fragmented into a large number of smaller platelets ..... OPHIOCERES

4. A single outer oral papilla, and two other oral papillae within, separated by intervals AMPHIURA

Paired infradental papillae present, and three other oral papillae on either side of the jaw, the outermost much the largest; radial shields contiguous .... AMPHIPHOLIS

Five oral papillae on either side of the jaw, all small, in a more or less contiguous series; oral shields short, triangular; radial shields not contiguous .... AMPHIOPLUS

Family *Ophiomyxidae*

Genus *Ophiomyxa* Mull. & Tr.

A single Rossian species.

Ophiomyxa brevirima H. L. Clark

Localities:

Lord Auckland Group:

Mainland (Bristow Island)

Crozier Point, among boulders at low tide, 1 specimen; coll. J. S. Jones, 10/9/43.

Tagua Bay, under boulders at low tide, 5 specimens; coll. W. H. Dawbin, 18/9/43.

This common New Zealand species had previously been taken at Carnley Harbour by Mortensen (1924).

Family: *Amphiuridae*

See above for a key to the three Rossian genera, *Amphiura*, *Amphipholis*, and *Amphioplus*, which are referred to this family.

Genus: *Amphiura* Forbes

KEY TO THE ROSSIAN SPECIES OF *AMPHIURA*

1. Oral side of disc naked .... *A. norae*

Oral side of disc scaled 2

2. Lower arm-spines of the middle region of the arm very much elongated .... *A. magellanica*

Not so 3

3. Two tentacle scales on the proximal part of the arm; arm spines 6 to 7 .... *A. amokurae*

One large tentacle scale; arm-spines 4 to 5 ..... *A. praefecta*

Amphiura norae Benham

According to Mortensen (1925, p. 395), this species occurs at Campbell Island, though he did not himself take it there, nor am I sure as to the basis of the record. No specimens are in any of the Cape collections.

Amphiura magellanica Ljungman

Localities:

Lord Auckland Group:

Mainland (Bristow Island)

No. 1 Station, Port Ross, among cast-up *Macrocystis* holdfast, also under boulders at low tide, 10 specimens; coll. W. H. Dawbin, 19/7/43.

Carnley Harbour; coll. D. Knowles and L. Pollock.

Tagua Bay, under stones at low tide, 10 specimens; coll. W. H. Dawbin, 18/9/43, 30/9/43.

Crozier Point, under sheltered boulders at low tide, 1 specimen; coll. W. H. Dawbin, 9/8/43. Also a second specimen, no date.

Ocean Island: in *Macrocystis* holdfast, 8 specimens; coll. W. H. Dawbin, 16/3/43.

Ewing Island: In coralline seaweed of rockpool, 1 spec., 11/8/43.

Remarks

This is a viviparous and hermaphrodite species. The specimen from Ewing Island taken in August proved to be carrying three young in the bursae. It is one of the few New Zealand echinoderms with a circumpolar distribution. Mortensen (1925) regards floating algae as a probable vector, and his opinion is perhaps strengthened by the two records above, in which a total of 18 specimens were collected from *Macrocystis*. Hence it is extremely dubious as to whether any other zoogeographic deductions should be made on the grounds of the occurrence of the species here or elsewhere. As to the colour in life in the Auckland Islands, Dawbin (private communication) makes the following notes: Colours variable—e.g., brown disc and blue-brown arms; red-brown disc and red-orange arms; fawn disc and darker fawn arms; grey disc and fawn arms, with dark grey rings. Specimens taken in Cook Strait are usually grey above and cream below.

Amphiura amokurae Mortensen (1925)

Localities:

Lord Auckland Group:

Mainland (Bristow Island)

Crozier Point, under sheltered boulder at low tide, 1 specimen, coll. W. H. Dawbin.

This is the only record obtained by the Cape Expedition. The species is endemic to the Rossian region.

Amphiura praefecta Koehler (1907)

This species was first found at Campbell Island by Filhol, but was not represented in the present collections.

Genus ***Amphipholis*** Ljungman

A single Rossian species, which is cosmopolitan.

Amphipholis squamata (Delle Chiaje) 1828

Localities:

Auckland Islands:

Mainland (Bristow Island)

Tagua Bay, under stones at low-tide level, 1 specimen; coll. W. H. Dawbin, 30/9/43.

Opposite Passage Island, in rock pool, 1 specimen; coll. J. S. Jones, 24/8/43.

Genus ***Amphioplus*** Verrill

A single Rossian species.

Amphioplus basilicus (Koehler) 1907

Localities:

Antipodes Islands:

Ringdove Bay, deep low-water pools, under stones, 6 specimens; coll. R. K. Dell, 7/11/50.

Campbell Island:

At low tide, below St. Col. Peak, 1 specimen; coll. R. W. Balham, 13/8/44.

Lord Auckland Group:

Bristow Island

Tagua Bay, under stones at low-tide level, 3 specimens; coll. W. H. Dawbin, 30/9/43.

Remarks:

This species appears to be one of the characteristic Rossian Ophiuroids, in that it has the widest distribution. It also reaches the South Island of New Zealand, but is not known outside the New Zealand region.

Family ***Ophiodermatidae***

A single genus in the Rossian region.

Genus ***Pectinura*** Forbes

Pectinura gracilis Mortensen 1924

Localities:

Lord Auckland Group:

Mainland (Bristow Island)

Tagua Bay, among stones at low tide, 2 specimens; coll. W. H. Dawbin, 20/1/43 and 19/8/43.

Shores of Musgrove Peninsula, littoral, 1 specimen; coll. C. A. Fleming, 1942.

Remarks:

This viviparous species was hitherto not known south of Stewart Island. The genus is also a new record for the Rossian region. *P. gracilis* is endemic to the New Zealand fauna.

Family ***Ophiolepididae*** Ljungman

A single Rossian genus.

Genus ***Ophioceres*** Koehler 1922

A single specimen collected in the Auckland Islands by Mr. W. H. Dawbin proves to be an undescribed species of *Ophioceres*.

Ophioceres marginata sp. nov.

(Plate 1, D and E; Fig. 5, A–E)

Dimensions: R, 18·5 mm.; r, 3·75 mm.; R/r, 4·8.

Colour: In life, light grey, fading in alcohol to cream.

Disc: Outline circular. Upper surface uniformly covered by rounded or polygonal, tumid plates, of varying sizes, not imbricating. Primary plates not distinct. At the interradial ambitus there is a row of four or five enlarged, prominent marginal plates. Radial shields small, elliptical, widely separated by a number of other plates, of which one lying on the radius is as large as each radial shield; it occupies the proximal apex of an almost equilateral triangle, of which the two radial shields occupy the other two angles. The lower surface of the disc is also covered by scales, smaller than those above, save at the ambitus, where a number of enlarged marginals occur. Genital clefts prominent, but very short, not extending beyond the first arm-segment. A few minute spinules occur around the genital clefts, but otherwise there is no spinulation on the disc either above or below (Fig. 5).

Buccal shields triangular, fan-shaped, the proximal angle slightly exceeding a right-angle, the sides straight, the distal border convex. Adoral plates subrectangular, about twice as long as broad, slightly broader without than within, each meeting its fellow broadly, within the shield. Oral plates evidently small, sunken, their outlines not visible externally. Five oral papillae, the outermost small and pointed, the second one the largest of the series and polygonal or subrectangular in shape, the third, fourth, and fifth smaller, subequal, often pointed. The unpaired proximal element rounded, larger than the proximal papillae, and overlain by them.

Arms: The lower arm-plates subpentagonal, only just contiguous, their proximal angle obtuse, their proximal and lateral borders concave, the lateral border housing the large tentacle-pore, the distal border convex. At the base of the arm these plates are at first broader than long, the distal convex border being especially broad, but towards the arm-tip they become more regularly pentagonal, about as broad as long, the distal border not notably greater than the other sides. The large tentacle-pore on either side bears a single, large rounded tentacle-scale, save in the case of the first arm-segment, where there is an additional minute internal scale. The arrangement of the lateral and

upper arm-plates conforms to the generic diagnosis in regard to the fragmention of the upper plates, and the division of the laterals into an outer spine-bearing portion and an inner portion devoid of spines. The details can be seen in the figures here given.

Arm-spines one to four in number, arranged in the following manner: The first two segments each carry one spine on each outer lateral,

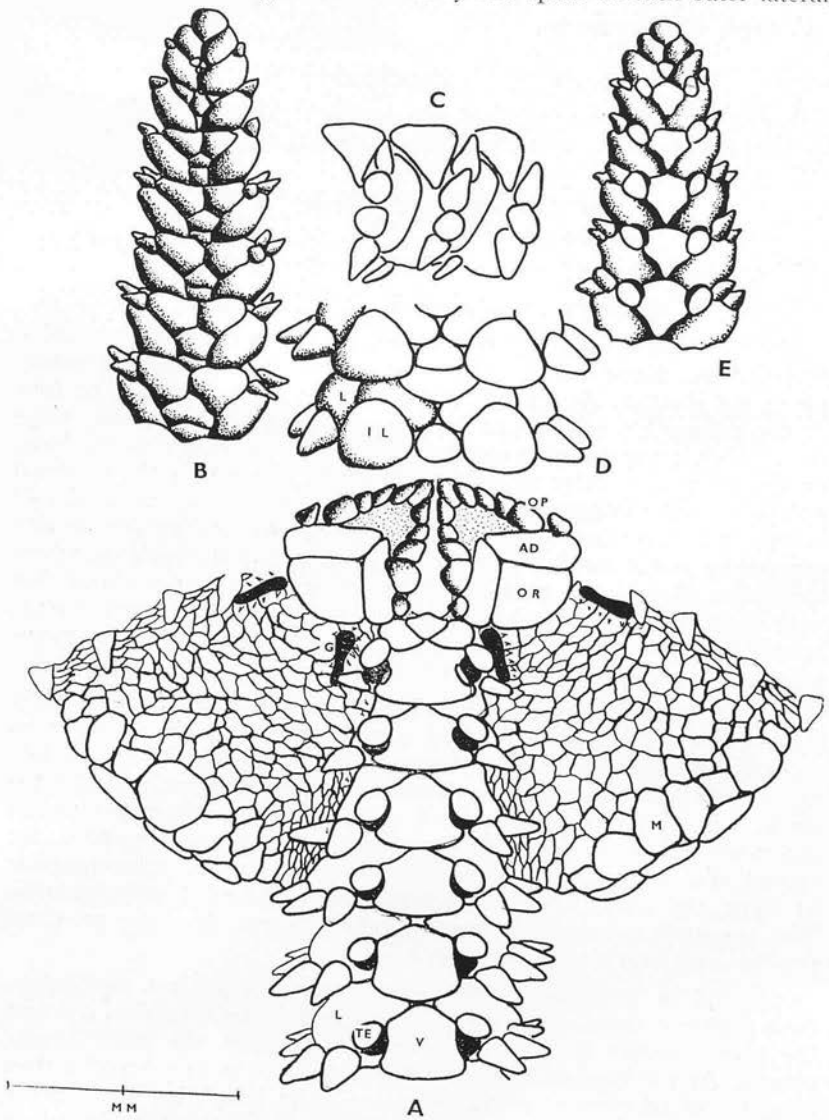

FIG. 5.—*Ophioceres marginata* sp.nov.: A, adoral aspect; B, aboral surface of arm near tip; C, lateral arm-plates and their spines; D, aboral plates of arm, near base; E, adoral plates of arm, near tip. Abbreviations: AD, adoral plate; IL, internal lateral plate; L, main lateral plate, bearing spines; M, enlarged marginal plate of disc; OP, oral papillae; OR, oral shield; TE, tentacle-scale; V, lower arm-plate.

the third segment carries two, the fourth carries three, the fifth and sixth carry four spines. Thereafter the number of spines is usually three, sometimes four, out to the eighteenth segment. Beyond that point the number is two or three, decreasing to one or nil in the cases of the final segments (the twenty-seventh and twenty-eighth in the holotype).

Holotype: In the Dominion Museum, Wellington.

Locality: French Island, Auckland Islands, in a rock-pool; coll. W. H. Dawbin, 25/8/43.

Remarks:

There are two previously known species of *Ophioceres*. One, *O. huttoni* (Farquhar), is endemic to the New Zealand mainland, ranging from Cook Strait to North Cape; the other, *O. incipiens* Koehler, is circumpolar, and is known from South Georgia, the Davis Sea, and from the Antarctic Ocean about 500 miles north of Adelie Land. The former species is littoral, the latter sub-littoral and abyssal. *Ophioceres marginata* is immediately distinguishable from the other two species by the number of its arm-spines (3 to 4, as compared with not more than two in the other species) and by its enlarged marginal plates (the marginals of the other two species being smaller than the inner disc plates). All three species agree as to the manner of subdivision of the lateral and upper arm-plates, and in having a genital cleft which does not extend beyond the first arm-segment. The latter feature is therefore probably to be treated as part of the generic diagnosis. On the other hand, the possession of only two arm-spines, a feature included by Koehler in his generic diagnosis, is not generic; nor, on the basis of comparative anatomy, would one expect it to be, the number of spines being usually variable within a genus.

Class: ***Echinoidea***

Genus ***Pseudechinus*** Mortensen

A single Rossian species.

Pseudechinus novae-zelandiae (Mortensen) 1921

Synonymy:

Echinus angulosus Farquhar (1898); Hutton (1904); Benham (1909).

Notechinus novae-zelandiae Mortensen (1921); Koehler (1926).

Pseudechinus novae-zelandiae H. L. Clark (1925); Mortensen (1943).

Localities:

Lord Auckland Group:

Enderby Island: Cast up on beach, 1 dried test; coll. J. S. Jones, 6/9/43.

Dundas Island: 1 specimen; coll. R. A. Falla, 28/10/43.

Mainland (Bristow Island)

Opposite Passage Islet, in shallow rock-pool, "spines khaki-coloured," 2 specimens; coll. R. W. Balham and W. H. Dawbin, 24/8/43.

Kekeno Bay, cast up on beach, 1 broken test; coll. E. F. Doley, 12/9/43.

Crozier Point, among boulders at low tide, 1 specimen; coll. R. W. Balham, 10/9/43. Between boulders at low tide, 1 specimen; coll. W. H. Dawbin, 9/8/43.

Waterfall Inlet, washed up on beach; coll. G. Lindsay, 1 dried test.

Tagua Bay, among rocks at low tide, 3 specimens; coll. W. H. Dawbin, 26/11/43, 27/11/43. On rocks at low-tide level, 1 specimen; coll. W. H. Dawbin, 22/10/43.

Bounty Island: 40 fathoms, 3 juvenile specimens; coll. R. K. Dell, 1950.

Remarks:

Although the species was previously known at Campbell Island (Mortensen, 1921) and Macquarie Island (Koehler, 1926), the above are the first records for the Auckland Group. The Bounty Island record is based on specimens only 3 mm. in diameter, and is therefore provisional. No echinoids were taken at Campbell Island by the Cape Expedition. So far as is known, this is the only echinoderm of the Rossian fauna which also occurs at Macquarie Island. Mortensen (1925) suggests that its pelagic larvae are perhaps responsible for its presence at the latter island—the species being a characteristically New Zealand one, not otherwise known from points not on the New Zealand plateau.

The species seems to reach its maximum size in the south. As may be seen from the accompanying graph (Fig. 6), the smallest specimens occur in the Cook Strait area, intermediate forms in the Forsterian region, the largest forms in the Rossian. Of the latter, specimens taken by the Cape Expedition at Tagua Bay prove to be by far the largest known, forming a cluster of points on the graph well apart from all other plots. No parasites were observed on these specimens. In view of their exceptional size, the following data are given for the Tagua Bay specimens:—

	Specimens			
	A	B	C	D
Horizontal diameter (cm.)	5·2	5·2	5·4	4·9
Height (cm.)	3·5	3·3	3·3	5·1
Diameter apical syst. (cm.)	1·0	1·1	0·9	0·9
Diameter peristome (cm.)	1·3	1·3	1·4	1·3
Width largest amb. plate (cm.)	1·1	1·3	—	—
Number of amb. plates	33	36	—	—
Width of largest interamb. plate	1·9	2·0	—	—
Number of interamb. plates	24	24	—	—
Largest spines (cm.)	—	0·7	0·8	0·7

Full data are not supplied for specimens C and D, as it was undesirable to denude all the specimens.

Apatopygus recens (M. Edwards)

Whilst examining echinoderms in the collection of the Dominion Museum, I located a single, very large specimen of this species labelled "Auckland Islands, Captain Bollons." There was no other evidence to confirm this label, which, unfortunately, may be unreliable. Since the species ranges as far south as Stewart Island, there is no reason to treat the record as improbable. The specimen is unusual in having exceptionally large gonopores, a fact that suggested to me the possibility

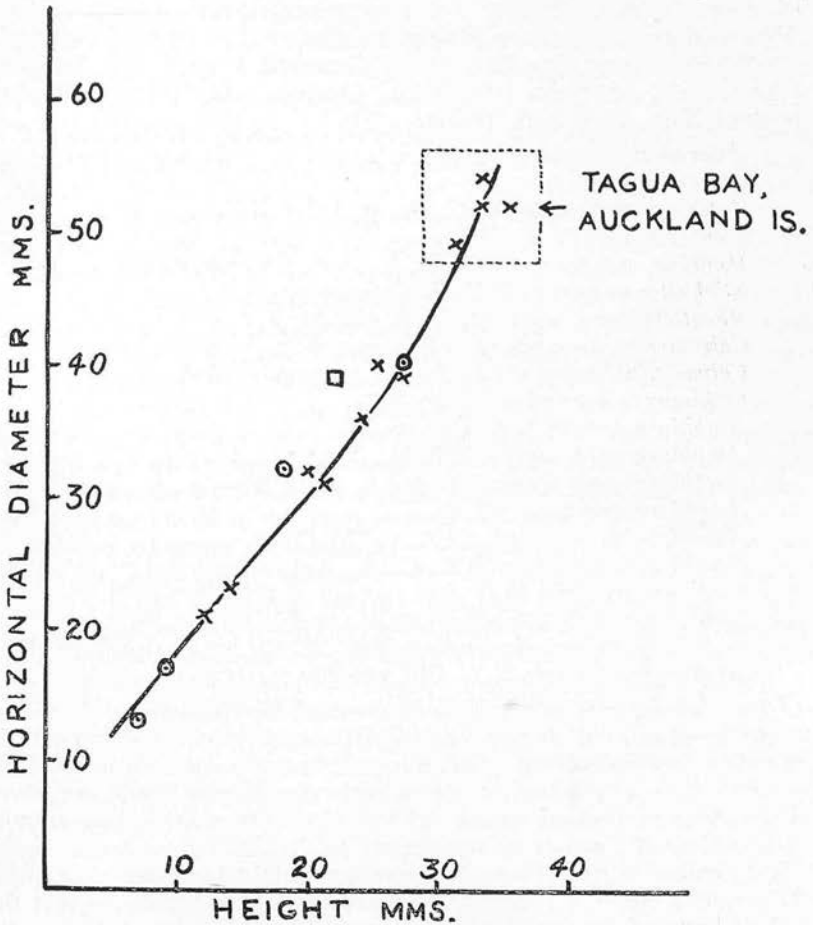

FIG. 6.—*Pseudechinus novae-zelandiae*: Variation of horizontal diameter with height. Cape specimens indicated by a cross, the group from Tagua Bay, Auckland Islands, being the largest known examples. The largest specimen recorded by Koehler (1926) from Macquarie Island is shown by a square. Mortensen's (1921) records from the New Zealand mainland area and Campbell Island are shown by circles.

of its representing a new species, perhaps of viviparous habit, or at least one producing a large yolky egg. However, I submitted a series of photographs of the specimen to the late Dr. Th. Mortensen, of Copenhagen, for comparison with the unrivalled collection of echinoid

material at his disposal, and he kindly informed me that there is one specimen from Cook Strait in the Copenhagen collections which has the same large size and relatively great height as the Bollons specimen, and that the gonopores show variation in size. He therefore concludes that the Bollons specimen is to be referred to the type species.

Origins of the Subantarctic Fauna

The following is the revised faunal list for the subantarctic islands of New Zealand, showing the geographical range of each species. Abbreviations: N.Z., New Zealand mainland; B., Bounty Island; M., Macquarie Island; S., Snares; C. Campbell Island; A., Auckland Island; Ant., Antipodes Island; Ch., Chatham Island; Cosm., Cosmopolitan; Mag., Magellanic region.

Asterodon dilatatus: N.Z., S.
Asterodon robustus: A.
Asterina aucklandensis: C., A., probably N.Z.
Henricia lukinsii: C., A.
Henricia compacta: N.Z., C., A., Ant., Ch., possibly S.
Stichaster australis: N.Z., S.
Allostichaster insignis: N.Z., S., A.
Calvasterias laevigata: C., A., Ant.
Calvasterias suteri: N.Z., S., C., A., possibly Ant.
Ophiomyxa breverima: N.Z., A.
Amphiura norae: N.Z., C.
Amphiura magellanica: N.Z., A., Mag.
Amphiura amokurae: N.Z., C., A.
Amphiura praefecta: C., A.
Amphipholus squamata: N.Z., C., A., Cosm.
Amphioplus basilicus: N.Z., C., A., Ant.
Pectinura gracilis: N.Z., A.
Ophioceres marginata: A.
Pseudechinus novae-zelandiae: N.Z., M., C., A., Ch., probably B.
Apatopygus recens: N.Z., Ch., possibly A.

Save for the one cosmopolitan species and the circumpolar *Amphiura magellicanica*, it will be seen that only *P. novae-zelandiae* occurs outside the New Zealand plateau; and, since the latter is unknown elsewhere save at Macquarie Island, it seems likely that it is an immigrant there from the New Zealand region. All the other species are either endemic to the New Zealand area, or endemic to the Rossian province of the New Zealand region. Thus, the more complete information now available merely serves to confirm Mortensen's (1925) conclusion that the echinoderms of the Auckland and Campbell Islands are not significantly related to any other region save New Zealand. As for the remaining islands, of which we now have some information, it is obvious that the echinoderms of the Antipodes Islands, so far as we know them, comprise a faunal assemblage similar to that of the Auckland or Campbell Islands. On the other hand, the Snares seem to be related more closely to the New Zealand mainland than to the other subantarctic islands; for, of the four genera known to have species there (omitting the unidentifiable record of *Henricia*), two are represented on the New Zealand mainland by identical species, and two others occur in the other

subantarctic islands as well as the New Zealand mainland, identical species being involved in each case. There are no Snares echinoderms which are shared with the other subantarctic islands and not also shared with the New Zealand mainland. Hence, so far as the asteroids, ophiuroids, and echinoids are concerned, the northern boundary of the Rossian marine province would fall south of the Snares; the latter would form a part of the Forsterian, with southern Otago and Stewart Island.

The above considerations, therefore, imply that the subantarctic islands of New Zealand have received their echinoderm fauna from an assemblage of species which has been the common heritage of all parts of the New Zealand submarine plateau.

As regards the problem of the more remote origins of that fauna, the subantarctic portion of it may perhaps be expected to offer some pointers. We must first eliminate from the discussion those genera which are cosmopolitan—namely, *Asterina*, *Henricia*, *Ophiomyxa*, *Amphiura*, *Amphipholis*, and *Amphioplus*. Of the remainder, *Ophioceres* does not occur outside the New Zealand and Antarctic regions; *Pectinura* has a wide Australian-Indo-Pacific distribution; *Pseudechinus* and *Allostichaster* are largely New Zealand and Australian, but have South American representatives; *Calvasterias*, *Stichaster*, and *Asterodon* have New Zealand and Magellanic, but not Australian, representatives. These facts suggest that *Pectinura* (in company with the other Indo-Pacific genera represented in the more northern part of the New Zealand region) arrived by way of some shallow-water path, such as that now found along the north-western margin of the Tasman Sea. The remaining genera constitute the main core of the Magellanic element in the New Zealand fauna, and may have entered the New Zealand region from the South American quarter, or could equally well have reached South America from New Zealand. The high proportion (about 80%) of endemic New Zealand echinoderms implies a long period of isolation. Furthermore, the fauna as a whole contains a far greater proportion of Australian-Indo-Pacific species than Magellanic species—16% as to 2% respectively. We may therefore conclude that, whereas an influx of forms from the Australian-Indo-Pacific direction has occurred unabated till recent times, and may very well still be taking place, on the other hand the South American sources of our echinoderm fauna long ago ceased to supply any appreciable elements. Broadly speaking, the South American affinities are not discernible below the generic level, a fact that suggests that faunistic contributions from that quarter have not been made during the latter part of the Tertiary, save in a few possible cases, such as *Amphiura magelianica*. Indeed, studies on the fossil echinoderms of New Zealand at present in progress have convinced me that even as early as the mid-Oligocene the New Zealand echinoderm fauna was predominantly Australian-Indo-Pacific in character. Since there is so clear a relationship between the echinoderm faunas of the New Zealand subantarctic islands and the rest of the New Zealand region, we may not be far wrong in supposing that a considerable part of their echinoderms came to the subantarctic islands by way of the New Zealand shallow-water link with the Australian-Indo-Pacific, and that most of the cosmopolitan genera have reached the area

by the same route, the South American route having ceased to provide contributions early in the Tertiary. This topic is further discussed in a paper on the origin of Australasian echinoderm faunas at present in the press (Fell, 1953).

ACKNOWLEDGEMENTS

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SUMMARY

The fauna of the subantarctic islands of New Zealand is known to include nine species of asteroids, nine species of ophiuroids, and one, possibly two, species of echinoids.

The Antipodes Islands genera are *Henricia*, *Calvasterias*, and *Amphioplus*; these are new records.

At Bounty Island occurs an echinoid, probably *Pseudechinus*.

Campbell Island genera are *Asterina*, *Henricia*, *Calvasterias*, *Amphiura*, *Amphipholis*, *Amphioplus*, and *Pseudechinus*. Of these, *Asterina aucklandensis* and *Calvasterias suteri* are new records.

The Auckland Islands are inhabited by *Asterodon*, *Asterina*, *Henricia*, *Allostichaster*, *Calvasterias*, *Ophiomyxa*, *Amphiura*, *Amphipholis*, *Amphioplus*, *Pectinura*, *Ophioceres*, *Pseudechinus*, and possibly *Apatopygus*. The new records are: *Asterodon robustus* sp.nov., *Amphiura amokurae*, *Pectinura gracilis*, *Ophioceres marginata* sp.nov., *Pseudechinus novae-zelandiae*.

The Snares Islands echinoderms comprise the genera *Asterodon*, *Henricia*, *Stichaster*, *Allostichaster*, and *Calvasterias*, of which all but *Henricia* are new records.

The Snares asteroids exhibit a closer relationship to the main islands of New Zealand than do those of any of the other islands. The remaining islands exhibit a distinctive fauna which, however, is more closely related to that of the main islands of New Zealand than to that of any other area. Two species only are common to these islands, to the Antarctic, and to South America, one of these being cosmopolitan, the other circum-polar. The evidence, therefore, does not support the concept of recent shallow-water connections between the latter regions. It is concluded that the fauna of the subantarctic islands is part of a common heritage shared by the whole New Zealand submarine plateau, that a considerable part of it has arrived by way of a shallow-water route from the Australian-Indo-Pacific regions.

Some data on the bionomics of the species involved are briefly presented. The genus *Asterodon* is extended to include *Diplodontias*, which name is suppressed.

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The Constitution and Relations of the New Zealand Echinoderm Fauna

By

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Colony No. 4. In December, 1946, Major G. A. Buddle succeeded in landing upon the formerly considered inaccessible North-East Island, which lies immediately to the North-East of Great Island. Here, amidst luxuriant vegetation dominated by the large puka, Major Buddle found *Placostylus bollonsi* to be quite abundant.

A point of special interest is that these snails are identical with those of the north-east colony on Great Island, in spite of the intervening waterway. North-East Island, however, showed abundant evidence of Maori occupation, and so it seems very probable that the Maoris either intentionally or unintentionally were responsible for acclimatising the snails to this island. The South-West King was visited by Major Buddle also, but no *Placostylus* was seen.

Considerations.

If the differentiation into three forms of *Placostylus* on Great Island is the result of induced isolation caused by Maori occupation during a period of at least three centuries, why is the North-East Island population identical with one of the colonies on Great Island? A probable reason may be that the utilization of the almost inaccessible North-East Island as a kitchen garden by the Maoris was a late development after the land on Great Island had deteriorated through over-cultivation.* The presence of stone contour walls to retard the washing away of the soil on the steep slopes of Great Island is sufficient evidence of the problem that beset the former Maori occupants.

GENERAL.

With all work on snail populations the determination of the length of time requisite for the development of a new form is the most difficult to assess. My present work, which is largely descriptive of existing colonies, provides a basis for future checks, but it is anticipated that the lapse of many years will be required to show any marked differences.

To return to *Paryphanta unicolorata* of the Seddonville flat, it may be noted that the type specimen collected in 1906, when the locality was in virgin bush, can be matched exactly with the present population of the area, which is persisting under greatly altered conditions.

THE CONSTITUTION AND RELATIONS OF THE NEW ZEALAND ECHINODERM FAUNA

By H. BARRACLOUGH FELL, Victoria University College, Wellington

External Relations of the Fauna.

TH. MORTENSEN (1925) has already given reasons for including in the New Zealand faunal region the Kermadec and Auckland–Campbell Islands as well as the Chathams and the main islands. Within the region thus defined, and taking into account eight species awaiting publication, there are known to occur 177 species. As is shown in the histogram (Fig. 1), 141 species (c. 80%) are endemic, 29 (c. 16%) comprise Australian and Indo-Pacific species, 4 (c. 2%) are Magellanic, and 3 (c. 2%) are cosmopolitan. The high proportion of endemic species may be correlated with the supposed prolonged isolation of the region; the external relations are chiefly with the Australian-Indo-Pacific faunas; the relation to the Magellanic region is very weak—and as shown later in this paper—occurs in the southern provinces only and in an area of mixed waters.

The above figures confirm Mortensen's earlier deductions, and as he has discussed the external relations in some detail, the main part of this paper is devoted to a survey of the internal constitution of the faunal region, based on fuller data on the distribution of echinoderms which are now available. It is obviously desirable to establish whether the echinoderms provide any evidence as to the existence of marine provinces within the New Zealand region. If such can be shown to exist, their relation to the distribution of other recent groups will be of interest; at the same time some further guide may be provided for palaeontological studies since echinoids are commonly found in the fossil state.

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*D'Entrecasteaux observed smoke rising from North-East Island in 1792.

Bathymetric Zonation.

Echinoderms generally exhibit a marked zonal distribution. The following bathymetric zones are customarily recognized:—

1. Littoral—
   (a) Eulittoral—0–50 metres
   (b) Sublittoral—50–200 metres.
2. Abyssal—200 metres and over

The majority of New Zealand echinoderms appear to be rather strictly stenozonal, i.e., each species is confined to a single zone. The few euryzonal forms are referred to later. There appear to be some 44 abyssal species. Since these cannot be utilised in delineating provinces, they are not further considered here, but for reference a check-list follows.

Check-list of Abyssal Echinoderms.

(a) Recorded hitherto only from Kermadec Islands:

Astroschema horridum
A. salix
Ophiacantha cornuta
O. vepratica
Ophioplinthaca plicata
Ophiomoeris clausa
Ophiurases obstrictus
Amphiura argentea
A. lanceolata
Ophiactis flexuosa
O. cuspidata
O. nama
O. canescens
Ophiochiton lentus
Ophiocoma brevipes
Ophiomusium scalare
Ophiophyllum petilum
Solaster torulatus
Phormosoma rigidum
Aglaometra incerta
Stiremetra breviradia
Thalassometra echinata
Glyptometra inaequalis
Charitometra basicurva
C. incisa
Metacrinus nodosus
M. wyvillii
Saracrinus varians
Diplocrinus alternicirrus
Hypalocrinus naresianus

(b) Recorded from near Kermadec Islands and from off East Coast of North Island:

Thaumatometra alternata

(c) Recorded from off North Cape:

Ophiocreas longipes
Astrotoma benhami
Ophiactis hirta

(d) Recorded from off East Coast of North Island:

Ophiacantha vilis
Ophiomastus tegulitius
Amphiophiura ornata
Homalophiura irrorata
Ophiocten hastatum
Ophiozonella stellata
Cosmasterias fragilis
Pourtalesia laguncula
Temnopleurus reynaudi
Pentametrocrinus semperi

Most of the above records were made by the Challenger Expedition from only a few stations. The lists may require augmentation by one or two species the zonation of which is dubious, and doubtless many species occur which are yet unknown.

Marine Provinces within the New Zealand Region.

If New Zealand echinoderms are listed according to their occurrence in the North Island, Cook Strait, South Island, Stewart Island, etc., no satisfactory grouping emerges; most of the species overlap geographically. As a result of molluscan studies, Finlay (1925 and later) has established certain marine provinces within the region. It is satisfactory to find that if the echinoderm distribution is compared with that of the mollusca a close measure of agreement is seen, save for some minor divergences to be noted below—probably attributable to incomplete data. The provinces may be considered from north to south in order, and stenotopic species designated for each. It should be noted that the check-lists must be regarded as provisional, as it is almost certain that a number of species at present known only from one province will later prove to be more or less eurytopic. On the other hand, any association of species generally corresponding with one or other of these check-lists—as may be found in late Tertiary strata—is likely to indicate environmental conditions approximating to those of the corresponding extant province.

Kermadecian Province. From the Kermadec Islands only a small eulittoral fauna is known. It includes a number of forms highly characteristic of the New Zealand region as a whole, but also includes six distinctive species which may be listed as stenotopic.

Amphiura kermadecensis
Petricia imperialis
Asterope lissotergum
Asterina oliveri
Astrostole rodolphi
Coscinasterias edmondi

Considering the Kermadecian fauna as a whole, 75% of its 11 species are forms endemic to the New Zealand region. The relationship with Australian-Indo-Pacific faunas is marked, comprising 21% of the fauna. There is no sign of any Magellanic element.

Aupourian Province. This province has been variously defined, but includes the northernmost part of the North Island. Echinoderm evidence would suggest that the southern boundary on the eastern side cannot fall north of Whangarei—for otherwise species such as *Asterodiscus truncata* and *Brisus gigas*, with distinct Australian-Indo-Pacific facies would present an anomalous distribution. The proportion of species occurring in the area north of Whangarei and endemic to the New Zealand region is 70%, a figure again lower than the average for the entire region. The stenotopic fauna may be listed at present as follows:

Eulittoral:

Cucumaria hollonsi

Sublittoral:

Astroceras elegans
Astroporpa wilsoni
Ophiothrix aristulata
Astropecten dubiosus
Asterodiscus truncatus
Ogmocidaris benhami
Aracosoma thetidis
Pseudochinus variegatus
Laganum depressum
Brissus gigas
Holothuria neozelanica
Cucumaria farquhari
Psolus neozelanicus
Comanthus novaezelandiae
Argyrometra mortenseni

In this province the relationship with Australian-Indo-Pacific faunas is most marked, comprising 27.5% of the entire fauna. Again, as in the case of the Kermadecian province, there is no discernible Magellanic element.

Cookian Province. This is taken as comprising the remainder of the North Island as well as Cook Strait and the northern half of the South Island. It is an area rich in species both eurytopic and stenotopic. The stenotopic species comprise 29, out of a total list of 74 littoral forms, and are as follows:

Eulittoral:

Amphiura aster
A. norae
A. rosea
A. annulifera
Diplodontias dilatatus
Stegnaster inflatus
Echinaster farquhari
Astrostole scabra
Arachnoides zelandiae
Cucumaria ocnoides
Phyllophorus longidentis
P. dearmatus
Caudina coriacea (also sublitt.)
Protankyra uncinata (also sublitt.)

Sublittoral:

Gorgoncephalus chilensis var. *novaezelandiae*
Ophiocentrus novaezelandiae
Amphiura sp. nov.
Ophionereis novaezelandiae
Ophiocoma sp. nov.
Pectinura sp. nov.
Ophiozonella megaloplax
Astropecten primigenius
Psilaster acuminatus
Persephonaster neozelanicus
Luidia varia
L. neozelanica
Eurygonias hylacanthus
Spatangus multispinus
Brissopsis zelandiae

The proportion of species endemic to New Zealand here reaches 78% of the entire littoral fauna for the province, a figure which approximates the average for the New Zealand region as a whole. The Australian-Indo-Pacific element shows a corresponding drop to 16%, also equal to that of the whole New Zealand region. Here for the first time a Magellanic element occurs, equal to some 3.4%. Thus the Cookian fauna, apart from its stenotopic forms, presents a broad section of the whole New Zealand echinoderm fauna.

Moriorian Province. Unfortunately, the evidence from echinoderms as to the existence of a distinct province for the Chatham Islands is completely negative. Only a small number of species are known, and all are eurytopic. The need for a survey of Chatham Islands echinoderms is obvious.

Forsterian Province. From the southern part of the South Island and Stewart Island a fauna of 46 echinoderms is known, but of these the great majority are eurytopic; the 8 stenotopic species are all eulittoral, as follow:

Ophiomyxa duskiensis
Ophionephthys stewartensis
Amphiura pusilla
Peridontaster benhami
Cucumaria huttoni
Pseudocucumis thompsoni
Psolidiella nigra
Comanthus benhami

Species endemic to New Zealand here comprise as much as 83% of the provincial fauna. The Australian-Indo-Pacific element falls to only 11%, a figure much below the average for the whole of New Zealand, while the Magellanic element is relatively high, being 4%. In other respects the province shows some resemblance to the Cookian, and possesses species in the Fiords area known otherwise only from the northern part of the Cookian province.

Rossian Province. Although the littoral fauna of the Auckland and Campbell Islands has been studied more closely in recent years, the total number of echinoderms remains small, namely 25. Of these, however, 6 are stenotopic, namely:

Eulittoral:

Amphiura praefecta
Asterina aucklandensis
Henricia lukinsii
Calvasterias laevigata
Cucumaria leoninoides

Sublittoral:

Chiridota carnleyensis

The proportion of endemic New Zealand forms in this province reaches the remarkably high figure of 92%. The Magellanic element remains low, 4%, though this is relatively high as compared with the whole New Zealand fauna. What is of interest is the complete absence of any Australian-Indo-Pacific element, elsewhere the chief external influence in the fauna.

Interrelations of the Faunal Provinces.

Histograms (Figs. 2–5) may be used to illustrate the faunistic interrelationships between the several provinces.

Endemic Species: Relatively greater effective isolation of the southern provinces is suggested by the peaking of endemic species there (Fig. 2). This is to be correlated with the distribution of Australian-Indo-Pacific species.

Australian-Indo-Pacific element: Fig. 3 illustrates the peaking of this element in the northern provinces, falling off evenly towards the south, disappearing in the Rossian. It suggests an influx from the north and north-east, the invasion falling off in the more distant southern areas, where presumably unfavourable environmental conditions serve as a barrier, especially to the larval forms. Palaeontological evidence would be desirable to show whether such an influx occurred in the past, or whether it is a process in active operation now.

Magellanic element: The Magellanic element (Fig. 4) presents a histogram almost the reverse of the preceding, though in all cases the figures are much lower. Presumably a minor incursion has occurred from the south-east, terminating in the Cookian, which forms the northern limit of the element. The species concerned are all such as could be transported by ocean currents either as larvae or on drifting material.

Cosmopolitan species: As might be expected, the proportion of such forms shows no significant variation, being uniformly low (Fig. 5).

Mixed associations: It is noteworth that the middle provinces alone contain all the above-mentioned elements. The variety of character of these faunas and their richness in species (especially the Cookian) may be interpreted as a consequence of the zone of "mixed waters" occurring there: *vide* Fleming (1944, p. 216).

Eurytopic Species.

Species occurring in two or more provinces number 127. It is not necessary to present a check-list of these here, though certain facts emerging from an examination of such a list may be noted. *Ophionereis fasciata*, a common endemic eulittoral ophiuroid, is known to occur in every province. The same appears true of the cosmopolitan *Amphipholis squamata*, though its presence in the Chathams requires verification. Other strongly eurytopic species include ***Amphiura amokurae***, ***Allostichaster polyplax***, ***Ophiomyxa brevirima*** and ***Evechinus chloroticus***. Since these species include some of the most characteristic New Zealand

forms (in the sense of being morphologically distinct from exotic forms) their wide distribution within New Zealand suggests their differentiation at a relatively early date. It is also noteworthy that, with the apparent exceptions of *Brissopsis luzonica* and *Ophiocreas constrictum* (known each from only one locality in New Zealand, though neither is endemic), all euryzonal species are also eurytopic. Since the two species named are widely distributed in the Pacific, a more widespread distribution in New Zealand is to be expected.

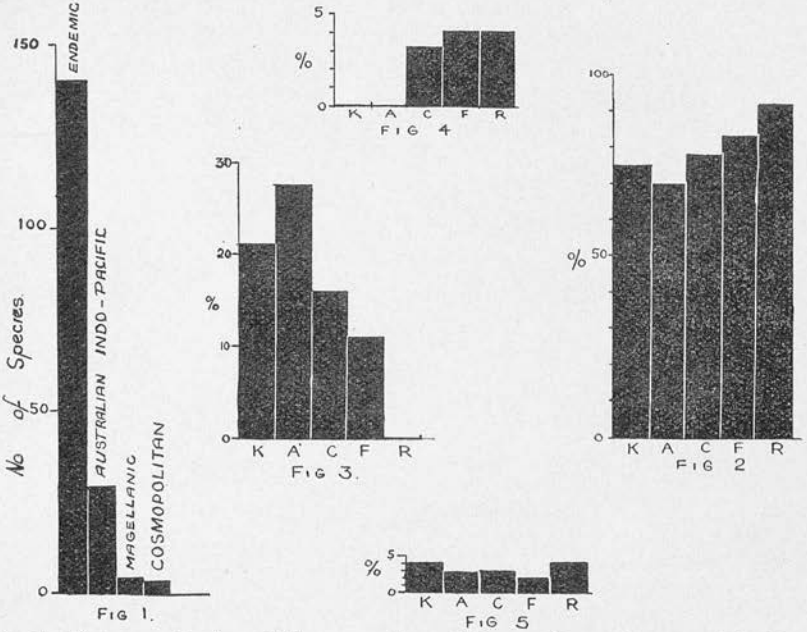

FIG. 1—Histogram showing relative proportions of the constituent elements of the New Zealand echinoderm fauna. FIGS. 2–5—Histograms showing incidence of constituent elements in provincial faunas, expressed as percentage of the total echinoderm fauna of each marine province. FIG. 2—Endemic element; FIG. 3—Australian-Indo-Pacific element; FIG. 4—Magellanic element; FIG. 5—Cosmopolitan element. In Figs. 2–5 the provinces read in order from left to right to correspond with their relative north to south disposition. Abbreviations: K, Kermadecian; A, Aupourian; C, Cookian; F, Forsterian; R, Rossian.

Acknowledgment.

I am indebted to Dr. A. H. Clark, of the U.S. National Museum, for assistance with the current nomenclature of New Zealand crinoids.

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OCEANOGRAPHY OF THE NEW ZEALAND SEAS

By A. E. HEFFORD, Chief Inspector of Fisheries and Director of Fishery Research, Marine Department, Wellington, New Zealand.

Introduction.

IF New Zealand's field of oceanographical interests be taken to be congruent with its political boundaries which reach as far north as the mandated territory of Samoa and as far south as the coasts of the Ross Dependency, it will cover a vast expanse of ocean roughly 4,000 miles long from north to south and about

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Rediscovery of the Ophiuroid Genus *Ctenamphiura* Verril

On September 10, 1874, H.M.S. *Challenger*, while dredging at Station 188, at the western end of Torres Strait, obtained from 28 fathoms two specimens of an amphiurid which afterwards became the genotype of the monotypic genus *Ctenamphiura*, receiving the name *Ctenamphiura maxima* (Lyman, 1879). It is remarkable among amphiurids for its robust build, the fact that the outer oral papillæ far exceed in size the infradental pair, for its very large tentacle scales, tumid disk and thick arms bristling with erect arm-spines arranged in dense comb-like masses. It has never since been seen, nor has any related form been discovered so far as I can determine. Of the only two specimens extant, one is in the British Museum, the other in the Museum of Comparative Zoology, Harvard.

Through the courtesy of Captain A. Black, Mr. W. H. Dawbin, of this Department, was able to dredge in Pelorus Sound in December 1951, when he obtained three specimens of an amphiurid, the affinities of which were not at first obvious. It differed remarkably from any other known New Zealand form. I now find that the Pelorus specimens (which were taken in 25–30 fathoms) conform in most respects with *Ctenamphiura maxima*, differing chiefly in the fact that the under surface of the disk is partly naked, and in the presence of only a single very large tentacle scale; also the massive arm-combs diminish in size on the proximal few plates. There seems no doubt that the species must be closely related to *C. maxima*, and, as the distinguishing features mentioned are diagnostic, it may take the name *Ctenamphiura dawbini* sp. nov. The type will be placed in the museum of this Department, and a full description, with figures, will appear in the "Zoology Publications from Victoria University College". Fortunately, the species comes from an accessible locality, from which, therefore, there is every likelihood of further material being obtained in the near future. It is hoped that at least a limited amount of material will soon be available for distribution to those museums which maintain important echinoderm collections.

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ECHINODERMS
from
SOUTHERN NEW ZEALAND

H. BARRACLOUGH FELL

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Echinoderms from Southern New Zealand

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Zoology Publications from Victoria University College, No. 18. Issued July, 1952.

ABSTRACT

Fifty species are discussed. Two genera, *Ctenamphiura* and *Ophiomisidium*, are reported for the first time from New Zealand. The former has hitherto been known only from two specimens of *Ctenamphiura maxima* (Lyman) which were taken by H.M.S. *Challenger* in 1874 in Torres Straits. Seven new sea-stars are described, *Henricia ralphae, Ctenamphiura dawbini, Amphiura heraldica, Amphioplus longirima, Ophiura chathamensis, Ophiomisidium irene, Ophiomastus stellamaris.* The presence of a large mixed population of *Psilaster, Persephonaster,* and *Sclerasterias* on the sub-littoral mud-banks off Cape Campbell is recorded. In the Southern Fiords, *Amphiura alba, Amphiura hinemoae,* and *Peronella hinemoae* are found to be present, all three species having previously been known only from northern New Zealand, and are still unknown from any intermediate point of the 700 miles of coastal seas which intervene. The ophiuroid *Pectinura maculata,* living in twelve to fifteen fathoms in Dusky Sound, was found to have been selectively feeding upon the anthers and pollen of Southern Beech (*Nothofagus*). Ecological data are given.

The collections upon which this paper is based number just under one thousand specimens of echinoderms from the off-shore and deeper waters of the southern half of New Zealand. They have been accumulated over the past five years from various sources, the chief of which are summarized below. One area of which our knowledge of echinoderm distribution has long been defective is the inaccessible south-western fiordland coast of the South Island. The relatively extensive collections from that region which are here recorded do much to fill the hiatus. However, new and interesting problems arise—such, for example, as the presence in the fiords of several species otherwise known only from the Northland and Hauraki Gulf coasts, some 700 miles away.

In a paper read before the 1947 New Zealand Science Congress (Fell, 1949), I attempted to assess Finlay's concept of New Zealand marine zoogeographic provinces in terms of echinoderm distribution, and gave lists of apparently stenotopic species for each of the proposed provinces. By that date, the *New Golden Hind* collections were already in my hands, and I drew upon the evidence they provided in preparing the lists, though without specifying the data upon which the statements were based. That data is now incorporated here, together with

that provided by subsequent expeditions. On revising the lists of species in the light of the new evidence, it is interesting to find that no amendments as yet appear necessary—apart from the addition of species since discovered. Meantime, therefore, the conclusions stated in that paper stand, and may be regarded as an approach to a working hypothesis. Material at present coming to hand from northern waters suggests that the zone of infiltration of Australian-Indo-Pacific echinoderms probably extends farther to the south than seemed to be the case in 1947, so that some adjustment of the boundary of the so-called Aupourian province may become necessary. That, however, is not relevant to the present study, which is concerned only with the southern part of New Zealand. It must also be stated that the holothurians still remain to be reviewed in the light of recent collections, a study at present in the hands of Mr. W. H. Dawbin. This paper is complementary to a similar one on the echinoderms of the sub-antarctic islands of New Zealand (at time of writing still in the press), and it is hoped later to provide a third contribution dealing with echinoderms from the northern waters of New Zealand.

Following are the chief sources of the material examined:—

(1) The *New Golden Hind* Expedition visited the south-western fiords early in 1946, collecting echinoderms from thirteen of the stations worked; the collectors were Messrs. H. W. Wellman and C. S. Wright, of the Department of Scientific and Industrial Research.

(2) The *Alert* (Captain A. J. Black) visited the north-west coast and the fiords regions of the South Island in May, 1950, and again in December, 1951, to January, 1952. Mr. W. H. Dawbin, of Victoria University College, collected echinoderms from twenty-two of the stations, assembling in all 360 specimens representing twenty-six species of sea-stars, echinoids, and crinoids.

(3) The Royal Research Ship *Discovery II* visited New Zealand in 1950, when, by courtesy of the National Institute of Oceanography, London, two New Zealand zoologists were enabled to observe on behalf of the New Zealand Oceanographic Committee. These were Lieutenant-Commander B. M. Bary and Mr. W. H. Dawbin, at whose request a dredging station was worked over the Chatham Rise (*Discovery* station 2733). A collection of ophiuroids obtained there by Mr. Dawbin was made available to me by the New Zealand Oceanographic Committee. A large, but fragmentary, Palaeopneustid echinoid, new to the fauna, was also taken; I understand, however, that an unbroken specimen of the same species was retained by the *Discovery* authorities for study in England, so the record is not discussed in the present paper.

(4) Various small, but valuable, collections have been made on my behalf by Lieutenant-Commander Bary at Stewart Island (also from one station of H.M.N.Z.S. *Lachlan*); by Miss P. M. Ralph, of Victoria University College,

from the eastern Canterbury and Otago coasts; by Mr. C. A. Fleming, who has secured several blocks of the Cook Strait sea-floor brought up in fishing-trawls, on which were echinoderms (ophiuroids). Mr. F. Abernethy, then of the *Phyllis*, made large collections of a limited number of species which apparently abound on the muddy, gently sloping shelf which lies east of Cape Campbell.

In addition to the generous help of the above-mentioned persons, specimens have also been brought in by Mr. J. A. F. Garrick. The generous co-operation of Captain A. Black made possible the *Alert* collections. I am indebted to Miss M. Wood, of the Royal Society of New Zealand, for facilitating my access to important and rare technical journals; to my wife, who undertook some of the tedious work involved when the mixed station hauls were being subdivided; to Dr. J. G. Gibbs and Mr. W. F. Harris, who identified plant remains in stomach contents; and to the New Zealand Oceanographic Committee for the material from Chatham Rise.

Ecology.—Environmental data have become sufficiently extensive to make it possible to offer a tentative classification of species under a variety of headings. Now that more detailed stratigraphical studies are being undertaken in New Zealand, the zoologist is frequently asked to suggest probable conditions under which fossils, especially Tertiary fossils, existed, using the present as a key to the past. The existing New Zealand echinoderm fauna finds its closest parallel in the late Tertiary strata of this country. Accordingly, some of the recent species of southern New Zealand are here grouped in the following categories, according to (*a*) physical character of the environment, (*b*) bathymetrical range. Forms with a marked preference are, of course, likely to be most useful.

Astrotoma waitei, Psilaster acuminatus, Persephonaster neozelanicus, and *Spatangus multispinus* indicate a mud-bottom in the sublittoral zone.

Astrobrachion constrictum, Amphiura rosea, Amphiura abernethyi, Ctenamphiura dawbini, and *Ophionereis novae-zelandiae* tolerate a mud admixture in a sandy or shelly substrate. All are littoral or sublittoral.

Pseudechinus huttoni, Pseudechinus albocinctus, and *Pseudechinus novaezelandiae* are littoral forms preferring a hard bottom, either rock or shell-sand detritus. Dead tests only have been dredged from mud admixtures. The latter species occurs in rock-pools and ranges down to 50 fathoms. The other two range from five fathoms to 50 fathoms.

Apatopygus recens, Peronella hinemoae, and *Echinocardium cordatum* are not known from a hard bottom, preferring a sandy substrate, the latter also tolerating mud admixture, and even mud alone.

The following tolerate a variety of environments except, apparently, mud: *Pentagonaster pulchellus, Ophiomyxa brevirima, Ophiomyxa duskiensis, Ophionereis fasciata, Pectinura maculata.*

Amphiura hinemoae occurs on any type of sand substrate, but is not yet known from either a hard bottom or from mud.

The following occur in all environments, from hard rock-bottom to soft mud: *Amphiura magellanica, Amphiura spinipes, Amphiura alba, Amphipholis squamata, Ophiactis resiliens, Ophiactis profundi, Pectinura gracilis, Asterina regularis, Sclerasterias mollis, Coscinasterias calamaria.* Except for *Asterina regularis,* which is not known from deeper than 15 fathoms, all these species occur through most of the littoral zone, and three of them—namely, *Amphipholis squamata, Ophiactis resiliens,* and *Ophiactis profundi*—extend beyond the continental shelf.

Evechinus chloroticus is essentially a hard-bottom form, occurring just below low-water mark. The solitary record given here of test-fragments from 50 fathoms is so contrary to experience that, until living material is obtained from that depth, the record should not be given too much value. The species will occasionally tolerate a soft muddy substrate, as, for example, the former Napier Inner Harbour before it was drained by the 1931 earthquake.

STATION LIST

Discovery station 2733:

Dredging on Chatham Rise, west of Chatham Islands, 300 metres; Lat. 43° 48′·0 S., Long. 178° 58′·0 W., November 4, 1950.

Lachlan station 367/51:

Bottom sample, Lat. 46° 17′·35 S., 170° 13′·4 E., 31 fathoms, off east coast of Otago, 1951.

New Golden Hind stations (all January–February, 1946):

NGH 1.—Preservation Inlet, Revolver Arm, 13 fathoms, mud.

NGH 2.—Preservation Inlet, Long Sound, 19–24 fathoms, mud and large shells; also shell sands.

NGH 3.—Preservation Inlet, Upper end narrow, Long Sound, 12–30 fathoms, shell detritus and sand.

NGH 25.—Chalky Inlet, Northport, 6–12 fathoms, sandy mud.

NGH 41A.—Chalky Inlet, Stella Cove, 7–10 fathoms.

NGH 44.—Dusky Sound, Cascade Bay, 16 fathoms, mud.

NGH 45A.—Dusky Sound, Facile Harbour, 14 fathoms, muddy sand.

NGH 56A.—Dusky Sound, Supper Cove, 20 fathoms, mud.

NGH 57A.—Dusky Sound, at mouth and centre of Wet Jacket Arm, three fathoms, rock.

NGH 64A.—Breaksea Sound, Harbour Island, four fathoms, sand.

NGH 82A.—Doubtful Sound, Shelter Island, 14 fathoms, muddy fine shell sand.

NGH L14.—Chalky Inlet, east shore, under limestone boulders at high-water mark.

NGH L15.—Doubtful Sound (not Dusky Sound, as stated by Fleming, 1950), Secretary Island, under rocks at low tide.

Alert stations:

1.—Pelorus Sound, 12–15 fathoms, fine viscid mud, December 26, 1951.

2.—Pelorus Sound, 25–30 fathoms, shell detritus and mud, Dec. 26, 1951.

3.—Across entrance to Pelorus Sound, fine mud, shell, and coral, 30 fathoms, December 27, 1951.

4.—West of middle Trio Island, fine mud, shell, and coral, 20 fathoms, December 27, 1951.

6.—One mile north-east of entrance to Kaiteriteri Cove, very fine gluey clay mud, 5 fathoms, December 30, 1951.

8.—Intertidal, Abel Head, at base of Farewell Spit, near high-tide level, December 31, 1951.

10.—Three miles south-east of Tonga Cove, Tasman Bay, South Island, fine gluey mud and shell detritus, 15 fathoms, January 1, 1952.

11.—Doubtful Sound, in passage between Bauza and Gaol Islands, ca. 50 fathoms, January 7, 1952.

12.—Gaol Passage, on south side of Gaol Island, Doubtful Sound, 50 fathoms, January 7, 1952.

13.—Dusky Sound, off Passage Point at south end of Acheron Passage, 12–15 fathoms, sand, January 8, 1952.

14.—Dusky Sound, 25–30 fathoms, fine sandy mud, January 8, 1952.

18.—Dusky Sound, in Nine Fathom Passage, 9–10 fathoms, January 10, 1952.

19.—Paterson Inlet, Stewart Island, immediately north of the south point of Kaipipi Bay, mud and sand, 5 fathoms, January 12, 1952.

20.—Paterson Inlet, Stewart Island, channel between Cooper Island and Bradshaw Peninsula, coral and shell, 18 fathoms, January 12, 1952.

22.—Doubtful Sound, 4–10 fathoms, May 2, 1950.

23.—Dusky Sound, Beach Harbour, hard bottom, 6–10 fathoms, May 5, 1950.

24.—Dusky Sound, Harbour at Big Petrel Island, 3–5 fathoms, May 5, 1950.

25.—Dusky Sound, Sealer's Cove, Anchor Island, 5 fathoms, May 5, 1950.

26.—Dusky Sound, Earshell Cove, 10–15 fathoms, mud, May 5, 1950.

29.—Preservation Inlet, near entrance, May, 1950.

32.—Doubtful Sound, 20–30 fathoms, May, 1950.

35.—Bligh Sound, on antipatharian coral, 30 fathoms, May 10, 1950.

Class **Asteroidea**

Fam. ASTROPECTINIDAE

Psilaster Sladen, 1885

Psilaster acuminatus (Sladen, 1889)

Ten miles south of Cape Campbell, 50 fathoms, March, 1947; coll. F. Abernethy; 377 specimens.

The above record is notable for the evidence it provides of the abundance of the species on at least one portion of the New Zealand continental shelf. It has hitherto been regarded as a somewhat rare, mainly deep-sea form (ranging down to more than 900 fathoms). It was taken by H.M.S. *Challenger* in the Tasman Sea, and has since been proved to have a wide southern distribution, though the individual records of its having been found total only six occasions. These indicate its presence off South Africa, off South and Eastern Australia, and on the New Zealand shelf. In addition to the above record, one other unrecorded instance is known to me—a specimen taken off Napier, said to have been in deep water (a statement which probably means no more than in the sublittoral zone); it is now in the Napier Museum.

In the large sample studied, only a single six-rayed specimen was discovered—a fact indicating unusually high stability of pentamerism for an asteroid. The colour of both the paxillar area and of the marginal plates is salmon-pink. As it occurs in company with the following larger species, it resembles superficially the younger stages of the latter; in *Psilaster*, however, only the infero-marginals bear spines, whereas in *Persephonaster* both series of marginals are so provided. *P. acuminatus* proves to be an excellent species for dissection by university classes, and has been so employed both at Victoria University College and at the University of Otago. It is notable for the very large size of its polian vesicles, structures which students commonly fail to discover in species more usually studied.

Persephonaster Alcock, 1891

Persephonaster neozelanicus Mrtsn., 1925

Ten miles south of Cape Campbell, 50 fathoms, mud, March, 1947; coll. F. Abernethy; 70 specimens.

There were no meristic variants in the population-sample studied. The largest individual measures: R, 140 mm.; r, 35 mm.; R/r, 4. The number of marginals to the interbrachial semi-arc is 49 in the same specimen. The species thus reaches a larger size than was hitherto supposed. Mortensen (1925), in describing the type material, stated that there was no anus observable in his specimen. In the present material, the anus is usually placed on a prominence in the centre of the

disc—some specimens have the rectal and pyloric portions of the intestine everted through it. Other new points that may be noted are: the sexes are separate; the gonopores open on the aboral inter-radii, near the margin. The colour in life is striking—the paxillar area salmon-pink, the marginals and underside cream.

Family LUIDIIDAE

Luidia Forbes, 1839

Luidia neozelanica Mrtsn., 1925

East Marlborough coast, off Mount Benmore, 40 fathoms, mud, in trawl, February 5, 1952; coll. J. A. F. Garrick; two specimens.

Family ODONTASTERIDAE

Asterodon Perrier, 1891

Asterodon miliaris (Gray, 1847)

Off eastern coast of Canterbury and Otago, between Taiaroa and Timaru, 40 fathoms, January and November, 1951; P. M. Ralph; seven specimens.

Colour in life, orange-buff. The features which distinguish the species from others of the genus in New Zealand are discussed elsewhere (Fell, 1952).

Peridontaster Koehler, 1920

Peridontaster benhami Mrtsn., 1925

Off coast of east Canterbury, between Moeraki and Timaru, 40 fathoms, January, 1951; P. M. Ralph; one specimen.

Since Mortensen described the type specimen, the species does not, till now, appear to have been taken again. The type locality was east of the South Island, possibly the same area as that from which the new specimen originates. The latter was orange in colour in life, though now faded to pale cream. It measures: R, 32 mm.; r, 22 mm.; ratio R/r, 1·45.

In comparison with the relative abundance of the diplacanthid species of *Asterodon,* the two monacanthid forms, namely, *P. benhami* and *Eurygonias hylacanthus,* are rare. Indeed, whilst the above is only the third record of *P. benhami, Eurygonias* is so far known only from the unique genotype-holotype described by Farquhar forty years ago, now preserved at Victoria University College.

Family GONIASTERIDAE

Pentogonaster Gray, 1840

Pentagonaster pulchellus Gray, 1840

Alert station 20, three specimens; and station 23, one young specimen.
Off east coast of Canterbury and Otago, between Taiaroa and Timaru, 40 fathoms, January and November, 1951; P. M. Ralph; seven specimens.

Bright orange-red in life, the large marginals coloured in the same way as the rest of the upper surface, paler below. In young individuals, the penultimate marginals are not yet enlarged; in the case of one of the east coast specimens, even at the stage having the major radius of 30 mm., the penultimate marginals are still not enlarged—an unusual circumstance which gives the specimen a very different appearance from normal.

Family ASTERINIDAE

Asterina Nardo, 1834

Asterina regularis Verrill, 1867

New Golden Hind stations NGH L14, one specimen, and NGH L15, two specimens.

Alert stations 2, three specimens; 6, one specimen; 19, three specimens; 24, one specimen.

These do not differ from the common form, and are similarly coloured.

Family ECHINASTERIDAE

Henricia Gray, 1840

Henricia ralphae sp. nov. (Figures 1 to 4)

Dimensions: R, 53 mm.; r, 15 mm.; breadth of arm at base, 17 mm. R, 54 mm.; r, 17 mm.; br., 23 mm. R, 64 mm.; r, 14 mm.; br., 13 mm. (syntypes). R, 72 mm.; r, 16 mm.; br., 18 mm. (holotype).

Arms, five. Abactinal and actinal surfaces of the arms covered by a thin ectoderm through which can be seen a meshwork of interlocking plates. These enclose papular areas of varying size, in most cases exceeding the area of an individual plate by at least five times. Papular areas polygonal, dark in colour (reddish-brown) when dried, bearing from one to five separate papulae. Some of the abactinal and lateral plates bear small, slightly raised pseudopaxillae which carry spines. They vary in number and arrangement as follows: On the disc, the majority of the plates are paxillose, and carry fascicular bundles of short, slender spines, from two to eight in number, but mostly four or five. Over the greater part of

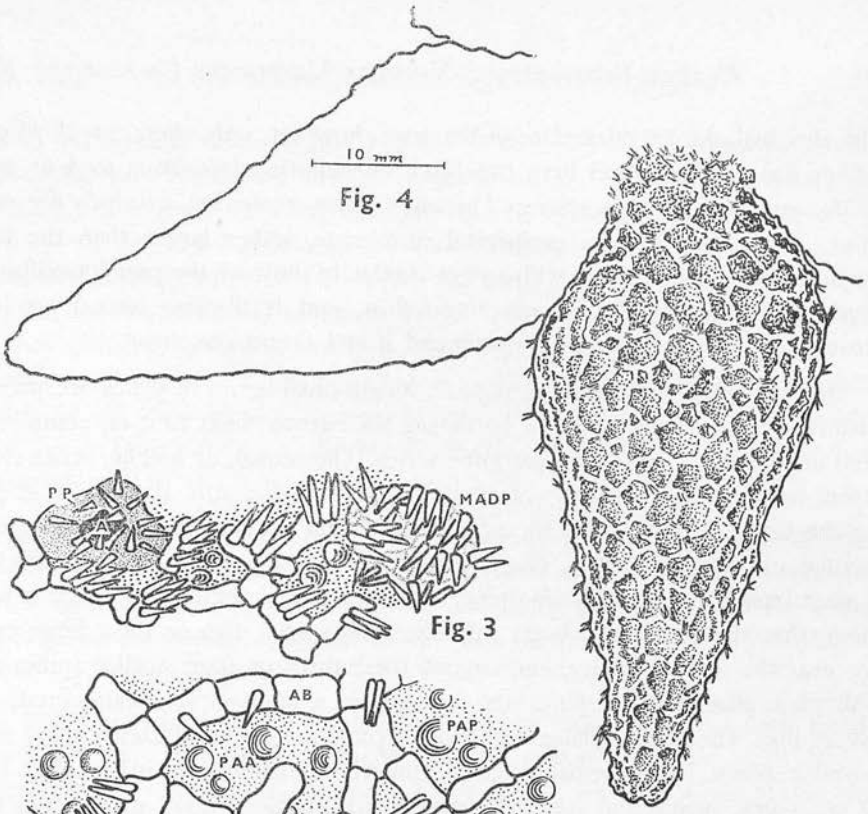


Fig. 4

Fig. 3

Fig. 2

Fig. 1

Henricia ralphae sp. nov.

Fig. 1.—Actinal surface of arm, the furrow lying to the left. Fig. 2.—Abactinal surface of arm. Fig. 3.—Abactinal surface of disc in region of periproct and madreporite. Fig. 4.—Part of syntype, showing the inflated type of arm, abactinal view.

Abbreviations: A, anus. AB, abactinal plate. ACT, actinal spines. AD, adambulacral spines. FU, furrow-spine of adambulacral plate. MADP, madreporite covered by spines. MAG, marginal spines, arranged in comb. PAA, papular area. PAP, papula (or dermal branchia). PP, periproct.

Figs. 1 to 3 are to the lower scale; Fig. 4 to the upper scale.

the abactinal and lateral surface of the arms, however, only about one-third of the plates are paxillose, and here the fascicles comprise from two to four spines, with occasional isolated spines. The anus, lying somewhat excentrically on the disc, is surrounded by a periproctal membrane, rather larger than the largest papular areas, and studded with spines similar to those of the pseudopaxillae. The madreporite lies nearby, in one interradius, and is likewise almost completely covered by spinules, which also surround it and almost obscure it.

On the actinal surface, three regular, longitudinal series of plates are present—namely, an adambulacral series bordering the furrow, next to it an actinal series, and next to this a prominent marginal series. The actinal, or middle, series extends from near the mouth to only about half-way along the arm. Papulae occur singly in the depressions between the adambulacral and actinal series, and between the actinal and marginal series. The armature of the plates is as follows: Each adambulacral plate bears a furrow-spine, which is placed deep in the furrow and is somewhat curved; it also bears subambulacral spines, two or three large ones at or near the furrow border, and beyond these three or four smaller spines occur. All these adambulacral spines are arranged in a more or less monoserial, transverse line. The actinal plates each bear a compact cluster of four or five similar slender spines. The marginal plates are transversely elongated; each of them carries a transverse monoserial comb of seven to ten slender, rather glassy spines with thorny tips. There are distinct intervals without spines between all these plates, so that in no case are there continuous transverse rows of spines extending from the furrow up the sides of the arm, such as occur in the other two New Zealand species, *H. lukinsii* and *H. compacta*.

Colour in life, brilliant orange-vermilion.

Holotype in the Zoology Museum, Victoria University College.

Type Locality.—Off east coast of Otago, between Taiaroa and Moeraki, three specimens trawled from 40 fathoms, collected by Miss P. M. Ralph in November, 1951. Syntypes from east coast of Canterbury, between Moeraki and Timaru, 40 fathoms, collected also by Miss Ralph in January, 1951.

Remarks.—This large and striking species of *Henricia* can easily be differentiated from the other two species of the genus occurring in New Zealand waters (*H. lukinsii* and *H. compacta*) by its sparse abactinal spinulation, its distinctive actinal and adambulacral armature, and by its large size. Of other species of *Henricia* known from the Southern Ocean, *H. obesa* (Sladen) resembles *H. ralphae* in general form, including the occasional inflation of the base of the arm (cf. dimensions of second syntype listed above with those of the holotype)—but it has a different spinulation. The same may be said of the Australian "*Henricia*

hyadesi" (Perrier), which supposed species Fisher (1940) has merged with *obesa* partim, and with *H. sufflata* and *H. compacta* partim. *H. sufflata* (Sladen) is as yet known only from the *Challenger* station 170, off the Kermadec Islands, 520 fathoms; it, too, has the base of the arm inflated in the type material, but the spinulation is quite different. *H. simplex* (Sladen) has a sparse abactinal spinulation, but its subambulacral armature differs from that of *H. ralphae*. *H. pagenstecheri* (Studer) presents one resemblance to *H. ralphae*, as also does *H. lukinsii*, in the presence of an interradial abactinal depression—an inconstant feature in the two former species, however—but that is the only similarity. *H. diffidens* (Koehler) is of the North Pacific *"longispina"* type, and so is not comparable.

The foregoing comparisons are given in view of the notoriously difficult systematics of *Henricia*. General body shape is variable and of no guide in separating species. The variation is well shown in the dimensions quoted for the present species. The pronounced inflation of the arm in one syntype is illustrated in Fig. 4.

In 1909, Benham described *Echinaster farquhari* from almost the same locality, namely, off Otago Heads, in 18 to 28 fathoms; only one specimen was obtained. In general facies it presents, to judge by Benham's account, a remarkable similarity to *H. ralphae*; in size and colour, it is similar. The conjunction of the localities caused me to wonder at first if he might have mistaken a *Henricia* for an *Echinaster*, and if the two might really be identical. It seems, however, that Benham's species must be a true *Echinaster*, as I think the following considerations show: Benham states that in *Echinaster farquhari* the abactinal armature of the plates of the arms comprises . . . "here and there an isolated, short, blunt, apparently immovable spine" which . . . "springs from a node in the network." His figures support the statement—which, of course, points to *Echinaster*. Again, although he refers to papulae on other parts of the body, he makes no reference to any between the actinal plates—a condition also diagnostic of *Echinaster*. There are a number of other differences between *E. farquhari* and *H. ralphae*, such as the distinctive arrangement of the spines on the lower plates, the fact that spines are sparse on the abactinal surface but become more numerous near the arm-tips; the madreporite in *E. farquhari* is prominent, projects above the abactinal surface, and is not surrounded by spines. We are forced to conclude that the two forms cannot be extreme variants of one and the same species, and that therefore the two related genera, *Henricia* and *Echinaster*, occur in the same area. An analogue is presented perhaps by *Persephonaster* and *Psilaster*, two related genera each represented by one species off Cape Campbell, and as yet known to be common only in that one place.

Family ASTERIIDAE

Sclerasterias Perrier, emend. Fisher, 1924

Sclerasterias mollis (Hutton, 1872)

Station NGH 3, one small individual.

Otago Harbour, November, 1951; coll. E. Batham; one specimen.

Ten miles south of Cape Campbell, mud bottom, 40 to 50 fathoms, March, 1947; coll. F. Abernethy; 100 specimens.

The species is abundant at Cape Campbell, and the hundred specimens taken there comprise only a representative sample of what came up in the trawl of the *Phyllis*. Of the hundred, 99 were five-armed, one alone six-armed. Two only showed regenerating arms, one of them in the so-called "sea-comet" condition. The colour in life is a bright brick-red, marked by longitudinal yellowish bands which correspond in position to the longitudinal rows of spines. The largest specimen has R, 120 mm.; r, 18 mm. The majority have arms exceeding 100 mm. in length. This is the only large *Asterias*-like starfish of New Zealand to have five arms. As the specific name indicates, it is very fragile, owing to weak regions of the body-wall where the arms enter the small disc.

Coscinasterias Verrill 1867

Coscinasterias calamaria (Gray, 1840)

Alert stations: 2, one specimen; 6, one specimen.

Off east Otago coast, 40 fathoms, two specimens.

The common eleven-armed starfish.

Allostichaster Verrill, 1914

Allostichaster insignis (Farquhar, 1895)

Alert stations: 23, fourteen specimens; 25, one specimen.

The widely-distributed, six-armed, fissiparous starfish of New Zealand. As it has already been recorded from Wellington, the Snares Islands, and Auckland Islands, its presence in the Fiords was to be expected. There, however, it was found only in Dusky Sound.

Class **Ophiuroidea**

Family OPHIOMYXIDAE

Ophiomyxa M. & T., 1842

Ophiomyxa brevirima H. L. Clark, 1915

Alert station 20, three specimens.

Disc dark purple-brown, arms banded with alternating 3 mm. bars of fawn and chocolate, light fawn below.

Ophiomyxa duskiensis Fell, 1947

Alert station 13, about twenty specimens; station 22, one specimen; station 23, four specimens.

New Golden Hind stations: NGH 2, three specimens; NGH 25, two specimens; NGH 41A, three specimens; NGH 57A, two specimens (type locality).

The *New Golden Hind* material has already been described (Fell, 1947). The *Alert* material, like the former, is uniformly small. The colour in life can now be stated—disc dark purple-brown, dark brown bands on the arm, in two shades of brown, turning dark grey in spirit.

Family TRICHASTERIDAE

Astrobrachion Doederlein, 1927

Astrobrachion constrictum (Farquhar, 1900)

New Golden Hind station NGH 64A, two specimens.

Alert station 35, one fragmented specimen.

Off Westland, 20 miles west of Hokitika, 216 fathoms, on branching coral; coll. H. W. Wellman; four specimens.

One of the *New Golden Hind* specimens is a uniform purplish-brown, save on the under-sides of the arms, which are paler. It is tightly coiled round an antipatharian coral (*Aphanipathes* sp., det P. M. Ralph). The other six specimens are of a variegated coloration, the aboral surface of the disc and the upper and lateral surfaces of the arms are creamy white; the adoral side is purplish-brown.

Family GORGONOCEPHALIDAE

Astrotoma Lyman, 1875

Astrotoma waitei Benham, 1909

Ten miles south of Cape Campbell, 40 to 50 fathoms, March, 1947, entangled in trawl-net; coll. F. Abernethy; five specimens.

Also same locality, 30 to 70 fathoms, February, 1952; J. A. F. Garrick; two specimens.

Off Westland, 20 miles west of Hokitika, 216 fathoms, on branching coral; coll. H. W. Wellman; one specimen.

In life, this species is a bright lemon-yellow. The creamy white colour mentioned by Benham is assumed after preservation. Its movements are slow and deliberate, and comprise mostly just coiling and uncoiling the arms in the vertical plane.

The eggs are very large and yolky, and range in size from 600μ to 1,000μ across —indicating direct development. The species may perhaps protect the brood, as

I find in one Cook Strait specimen a cluster of eggs in a layer one-deep on the fourth, fifth, and sixth segments of one arm.

The number of arm-spines and their arrangement varies somewhat more than Benham indicates in his original description. Each arm-segment bears on either side from eight to ten short, cylindrical, blunt spines. The spines each terminate in a tuft of glassy spicules. In the outermost quarter of the arm, the spines decrease gradually in number till only one or two remain; the outer (that is, morphologically upper) spines of the segments are the ones that persist to the end of the arm.

Family OPHIACANTHIDAE

Ophiacantha M. & T., 1942

Ophiacantha vilis Mrtsn., 1924

Off Cape Campbell, 50 fathoms, 1947; coll. F. Abernethy; one specimen.

The species has hitherto been known only from one record, that of the type material, which was taken in Cook Strait from 200 fathoms. That its range extends upwards to include the sublittoral region of the continental shelf is now evident; apparently, however, it is rare, since only one specimen was taken out of hundreds of other echinoderms trawled in the same area at the same time.

The specimen shows little sign of the outer lobe of the oral shield mentioned by Mortensen (1924), but in other respects it agrees. The species reaches a larger size than was hitherto supposed. In the present case, the radius of the disc is 3·5 mm., the major radius ca. 30 mm., giving the ratio R/r 8·5; thus the proportions noted by Mortensen are retained.

Family AMPHIURIDAE

Amphiura Forbes, 1842

Amphiura magellanica Ljungman, 1866

Alert station 13, seven individuals.

Off Cape Campbell, 50 fathoms, April 4, 1947; coll. F. Abernethy; five individuals.

In fresh material of New Zealand examples of this species, the colour seems relatively invariable—the disc is grey above, cream below, the arms being entirely cream-coloured. In the field, therefore, it provides a useful diagnostic feature for separating the species from the very similar following one, where brilliant shades of various colours occur, often with banding on the arms.

In spirit material, it may be noted that in adult specimens of *Amphiura magellicana* the disc is usually tumid above, on account of the presence of embryos in the bursae—an additional difference to those already cited by Mortensen (1924) as distinguishing it from the following nearly-related form.

Amphiura spinipes Mrtsn., 1924

Alert stations: 4, three specimens; 13, five specimens; 14, one individual; 20, about forty specimens.

Lachlan station 367/51, one specimen.

Amphiura spinipes is extraordinarily variable in respect to its coloration, even within populations of relatively restricted area—for example, *Alert* station 20 (Paterson Inlet, Stewart Island). On preliminary macroscopic sorting of the collection from the latter station, four distinct lots were isolated, on account of colour differences, which afterwards proved to be all of this species. Following are some of the major colour variants noted:—

(*a*) Purple-brown disc and arms—ten individuals from station 20.

(*b*) Pinkish-fawn above, arms pale fawn below—about twenty individuals from station 20.

(*c*) Grey, the arms banded with narrow black bars at 2 mm. intervals—one individual from station 4.

(*d*) Disc dark fawn, arms brilliant orange-vermilion—about twelve individuals from stations 13 and 20.

(*e*) Disc brownish-orange, arms fawn, with narrow black bands at 2 mm. intervals—two specimens from station 20.

Amphiura rosea Farquhar, 1894

Alert stations: 1, six specimens; 3, five young individuals; 6, three individuals.

In the present instance, all material was in spirit before it was examined, so the colours were not noted. Specimens from *Alert* station 3 are of typical form, but small. Those from station 1 have the radial shields separated by more scales than in the case of Farquhar's type.

Amphiura hinemoae Mrtsn., 1924

Station NGH 64A, one specimen.

Alert station 14, ten specimens.

Colour—hitherto unknown from fresh material—pale pink or orange, the disc naked below, the primaries prominently pigmented with grey spots.

The type locality—and, indeed, hitherto only known one—is White Island, 55 fathoms. Thus, again, as in the case of *Peronella hinemoae,* the southern range of the species is extended by some seven hundred miles, yet no occurrences are known in the intervening waters.

Amphiura amokurae Mrtsn., 1924

Paterson Inlet, Stewart Island, intertidal, under stones on seaward side of Point Anglem, January, 1951; coll. B. M. Bary; a single specimen.

The species appears to be nowhere common, though isolated instances establish its presence throughout New Zealand from North Cape to Auckland Islands. Only one specimen was obtained by the Cape Expedition (at Auckland Islands).

Amphiura alba Mrtsn., 1924

New Golden Hind stations: 44, one specimen; 2, two young specimens.
Alert stations: 18, two specimens; 20, one specimen.

The above specimens agree with *A. alba* in having one triangular tentacle-scale, no disc spines, the oral side of the disc completely scaled, spearhead-shaped oral shields, five or six pointed arm-spines, and the outer oral papilla large, flattened, and pointed distally. On the other hand, the six primary plates of the upper side of the disc are quite distinct—of rounded form—each separated from its fellows by smaller disc-scales. In Mortensen's type (from Colville Channel, 35 fathoms), the primaries are said to be "not very distinct." The difference, however, may be due only to age.

We have here yet another instance of a northern New Zealand species occurring seven hundred miles to the southward without known intervening records.

Amphiura abernethyi Fell, 1951

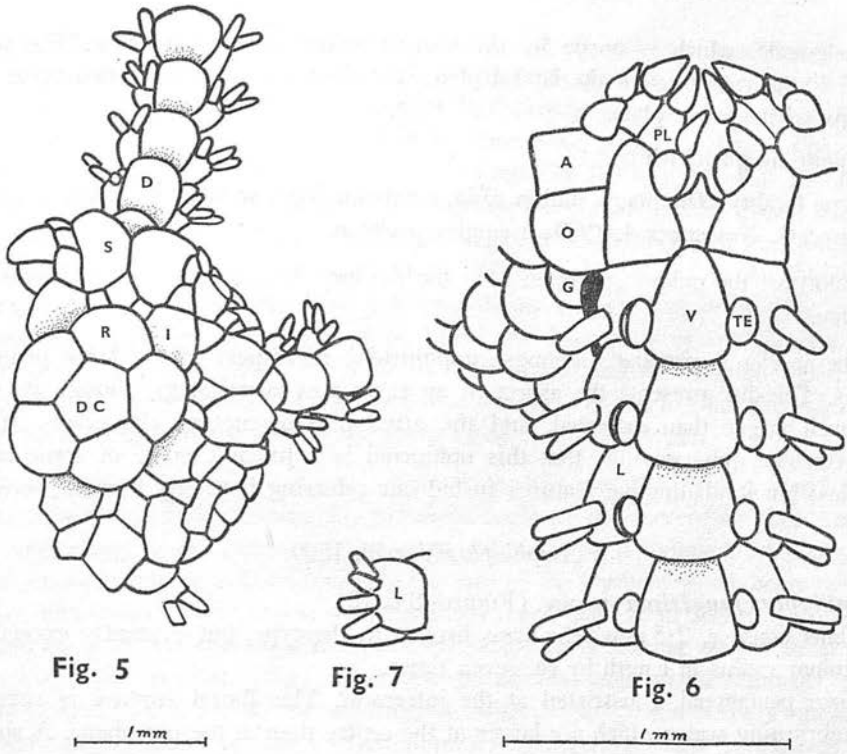
Alert stations: 10, six specimens; 26, one specimen.

These specimens are all only some two-thirds as large as the type material (from Cape Campbell). They are therefore more directly comparable with the related *A. norae*. Also, the number of mosaic platelets between the radial shields (about 18 to 20) is smaller than in the type *A. abernethyi*, though still considerably exceeding the corresponding number (5 to 7) in *A. norae*. The spacing between the radial shields is not so great in the present material as it is in the type, again a feature reminiscent of *A. norae*. It would not be surprising if eventually it should be found that *A. abernethyi* and *A. norae* are the two limiting forms of a cline.

Amphiura heraldica sp. nov. (Figures 5 to 7)

Dimensions: R, 8·0 mm.; r, 2·9 mm.; ratio R/r, 2·8.

Disc, circular, flattened, its aboral surface covered by scales of various sizes, amongst which the primaries and the radial shields are prominent. The scales partly imbricate and partly interlock. The six primary plates—namely, the dorso-central and the five radials—are large, contiguous, extend from the centre to half-way to the periphery, and shape the pattern of the English heraldic tudor rose. Adjoining the radial primaries, and interradial in position, occur five irregularly pentagonal plates, one to each interradius, and evidently also belonging to the primary system. Adjoining the radial distal border of each primary radial plate there are three small scales arranged as a trefoil, the middle leaflet of which is inserted between the proximal ends of the two adjoining radial shields. The radial



Amphiura heraldica sp. nov.

Fig. 5.—Aboral view. Fig. 6.—Adoral view. Fig. 7.—Lateral view of arm-segment. Figs. 5 and 7 to scale at left; Fig. 6 to scale at right.

Abbreviations: A, adoral plate. D, upper arm-plate. DC, dorso-central primary plate of disc. G, genital cleft. I, primary interradial plate of disc. L, lateral arm-plate. O, oral shield. PL, oral plate. R, primary radial plate of disc. S, radial shield. TE, tentacle-scale. V, lower arm-plate.

shields are polygonal, about as broad as long, mutually contiguous. The rest of the aboral surface of the disc is covered by rather large plates, smaller, however, than those already mentioned, and disposed in a less regular manner. The adoral surface of the disc is clothed in coarse, imbricating scales. Genital clefts extend to the second arm-segment. Oral shields subtriangular, with a proximal acute angle and a distal convex base. Adoral plates subtriangular, larger than the oral shields, meeting broadly (or even overlapping) within. Three pairs of oral papillae, one pair infradental, one pair carried on the oral plates, the outermost borne on the adoral plates. All the oral papillae are large, leaf-shaped, and the two inner pairs have pointed tips.

Arms: upper arm-plates as broad as long, subquadrate, each with a convex distal border overlapping upon the next plate, all broadly contiguous. Lateral plates meeting neither above nor below, each bearing four, short, stout, subequal spines. Lower arm-plates similar to upper arm-plates, save for the first one, which is more elongate. Tentacle-pores large, each having one large elliptical flat

tentacle-scale, which is borne by the corresponding lower arm-plate. The pore itself is excavated within the lateral plate, and does not encroach much upon the margin of the lower plate.

Colour in spirit, white.

Type locality: *Discovery* station 2733, Chatham Rise, west of Chatham Islands, 300 metres, November 4, 1950; a single specimen.

Holotype: the unique specimen is in the Zoology Museum, Victoria University College.

The species is peculiar (amongst amphiurids) in respect of the large primary plates. The disc presents the aspect of an early post-larval stage, though its size is much larger than expected, and the arms present mature characters. It is, nevertheless, quite possible that this ophiuroid is a juvenile stage of some large species; but its distinctive features forbid our referring it to any known species.

Amphioplus Verrill, 1899

Amphioplus longirima sp. nov. (Figures 8 to 10)

Dimensions: r, 2·5 mm., the arms broken in the type, but evidently exceeding the minor radius in length by ca. seven times.

Disc: pentagonal, constricted at the interradii. The aboral surface is covered by imbricating scales which are larger at the centre than at the periphery. A single

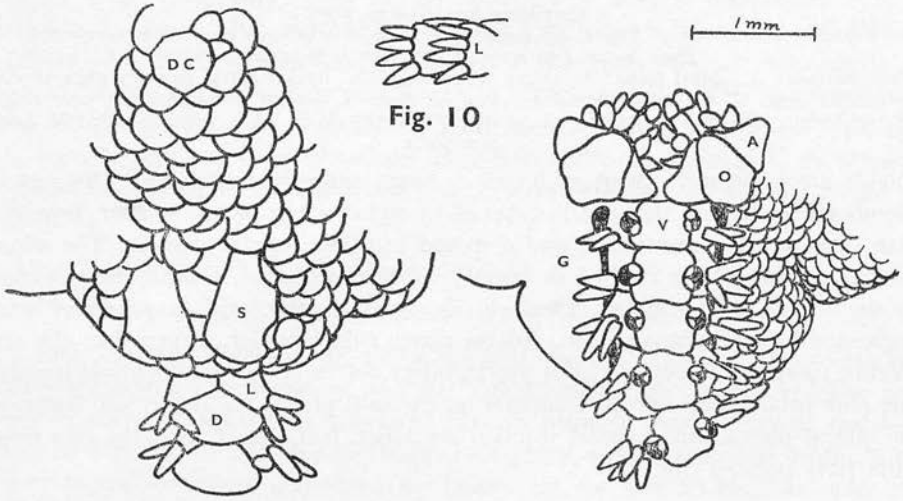


Fig. 8 Fig. 10 Fig. 9

Amphioplus longirima sp. nov.
Fig. 8.—Aboral view. Fig. 9.—Adoral view. Fig. 10.—Lateral view of arm-segment. All to scale shown.
Abbreviations: A, adoral plate. D, upper arm-plate. DC, dorso-central primary plate of disc. G, genital cleft. L, lateral arm-plate. O, oral shield. S, radial shield. V, lower arm-plate.

dorso-central primary plate is distinguishable. Radial shields reaching to only about one-third of the distance from the ambitus to the centre, more or less bean-shaped, almost contiguous distally but divergent proximally at an acute angle; the intervening angle is filled in by about four polygonal plates. The inter-radial borders of the radial shields are overlapped by the neighbouring disc-scales. Adoral surface completely scaled, the scalation finer than on the aboral surface. Genital clefts extending to the fourth arm-segment. Oral shields of the spearhead-shaped type, but modified, the inner extremity (i.e., the "point" of the spearhead) being rounded, not angular. The oral shields are longer than broad. The adoral plates are triangular, meeting within. There are four pairs of oral papillae, one pair infradental, one pair carried by the oral plates, and the two outer pairs are borne by the adoral plates. All the oral papillae are leaf-shaped, but the outermost have pointed tips, and evidently are really of the spiniform type.

Arms: upper arm-plates broader than long, subtriangular, with a broad distal convex border which overlaps the proximal angle of the succeeding plate, save in the first upper plate, where the proximal obtuse angle is exposed. Lateral plates meet neither above nor below, save in the case of the segment which bears the first upper arm-plate (segment five when counted from below); in this case the lateral plates meet in the midline above. Lateral plates each bearing on the basal arm-segments four similar, stout, short spines; on the more distal segments, three spines only. Lower arm-plates subquadrate, with concave distal borders and lateral borders emarginated by the tentacle-pores; neighbouring plates contiguous over most of their width. Tentacle-pores large, having two similar leaf-shaped tentacle-scales on the inner side, both scales being carried, therefore, by the corresponding lower arm-plate.

Colour, in spirit, white.

Type locality: *Discovery* station 2733, Chatham Rise, west of Chatham Islands, 300 metres, November 4, 1950; a single specimen.

Holotype: the unique specimen is in the Zoology Museum, Victoria University College.

This, only the second species of *Amphioplus* to be discovered in New Zealand waters, appears to be more closely related to its New Zealand congener *A. basilicus*, than to any other Pacific or Antarctic form. It can, however, be easily distinguished from *A. basilicus* by the following: (1) the long genital clefts (to which the specific name refers)—these reach to near the ambitus, whereas in *A. basilicus* they do not pass beyond the first arm-segment; (2) the oral shields are spearhead-shaped, whereas they are triangular in *A. basilicus*; (3) the radial shields are somewhat larger and more widely separated. Of the six known Australian species, only *A. stenaspis* and *A. didymus* seem at all comparable; but the former is distinguished by its long, slender, radial shields, the latter by its larger inner tentacle-scale.

Amphipholis Ljungman, 1867

Amphipholis squamata (Delle Chiaje, 1828)

Alert station 12, one specimen.

Also Island Bay Shelf, ca. 100 fathoms, July, 1950; C. A. Fleming; one specimen.

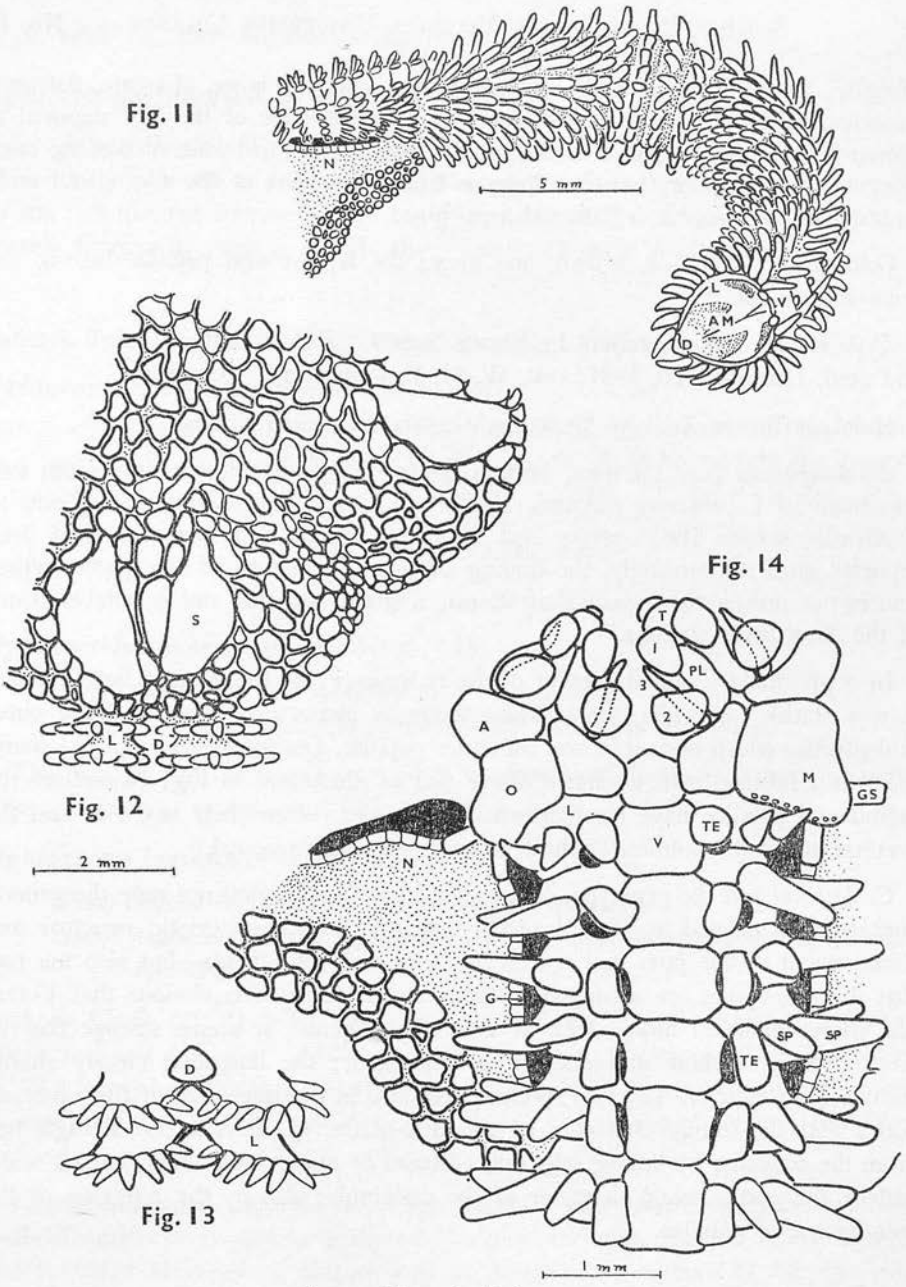
Ctenamphiura Verrill, 1899.

Ctenamphiura dawbini Fell, 1952 (Figures 11 to 14)

Dimensions: R, 60 mm.; r, 6 mm.; ratio R/r, 10.

Disc: rounded-pentagonal, constricted at the interradii, tumid, robust. Aboral surface covered by a coarse, uneven mosaic of lumpy, thick plates, in the manner of cobblestones, none imbricating, and of smaller size in the interradii. No primary plates. Radial shields longer than broad, pearseed-shaped, separated by a wedge of about six mosaic plates; extending from near the periphery to about one-third of the distance to the centre. Adoral surface of the disc naked, save at the subambital border, and save for scales bordering the genital clefts. The subambital plates are uneven, thick, and lumpy like those above. The genital clefts extend to the fifth arm-segment. The oral shields are large, spearhead-shaped, longer than broad, with an obtuse proximal angle; their distal borders abut upon the outer genital scales, their lateral borders rest upon the first lateral arm-plates, their proximal borders alone adjoin the adoral plates. Adoral plates triangular, small, meeting neither within nor without. Three pairs of oral papillae; an infradental pair, flattened, scale-like, large, placed vertically upon the torus, and hence viewed end-on and so appearing smaller than in reality; an apparent outer pair, which, however, are really an intermediate pair, scale-like, very large, rounded, carried by the adoral plates; and an outermost spiniform pair, long, carried on the adoral plates, but reflexed within the oral cleft so as to be partly hidden by the large and apparent outer papillae.

Arms: robust, compressed, densely invested by erect arm-spines. Upper arm-plates small, fan-shaped, with a proximal angle and a distal convex border, contiguous—largely obscured by the uppermost arm-spines which curve over to meet in the midline. Lateral arm-plates meeting neither above nor below, each provided with eleven or twelve erect, stout arm-spines arranged in a continuous comb. As the arm is unusually robust, the segments are much broader than long, and consequently the arm-combs of succeeding segments are crowded together to form a dense bristling armature. The arm-combs of those segments which underlie the disc are smaller, and comprise fewer spines; the number of the latter decreases from without inwards till at the first segment there are only two spines. The number of spines in the combs at the distal ends of the arms, on the other hand, remain fairly constant almost to the extremities. Lower arm-plates subquadrate, with slightly concave distal borders, broadly contiguous. Tentacle-pores large,



Ctenamphiura dawbini sp. nov.

Fig. 11.—Proximal half of arm viewed obliquely, mainly from below. Fig. 12.—Aboral view. Fig. 13.—Portion of arm, viewed from above at a point where the arm is downwardly flexed, exposing the arm-plates more fully than in Fig. 12. Fig. 14.—Adoral view.

Fig. 11 to upper scale; Figs. 12 and 13 to scale at left; Fig. 14 to lower scale.

Abbreviations: 1, first, or infradental, oral papilla. 2, second, or apparent, outer papilla. 3, third, or true, outer papilla, reflexed below second papilla. A, adoral plate. AM, ambulacral vertebra. D, upper arm-plate. G, genital cleft. GS, outer genital scale. L, lateral arm-plate. M, madreporite. N, naked adoral interradial region. O, oral shield. PL, oral plate, S, radial shield. SP, arm-spine. T, tooth. TE, tentacle-scale. V, lower arm-plate.

elongate, almost as long as the arm-segments, with one large, elongate, flattened tentacle-scale borne by the lateral plate. The tentacle-scale of the first segment is rounded, that of the second bean-shaped, that of the third and succeeding ones elongate, quadrangular, twice as long as broad, broadest at the free distal end; so large as to resemble a flattened arm-spine.

Colour: mottled fawn, brown, and grey; the largest oral papillae brown, the arms whitish below.

Type locality: *Alert* station 2, Pelorus Sound, 25 to 30 fathoms, shell detritus and mud, December 26, 1951; coll. W. H. Dawbin; three specimens.

Holotype: in the Zoology Museum, Victoria University College.

Ctenamphiura has, till now, been a monotypic genus known only from two specimens of *C. maxima* (Lyman, 1879) which were taken from 28 fathoms at *Challenger* station 188, western end of Torres Strait. No specimens had been reported since; accordingly, the finding of three specimens of the genus, representing an undescribed species of it, was a great surprise and a notable result of the *Alert* investigations.

In a preliminary announcement of the rediscovery of the genus (Fell, 1952a), it was stated, *inter alia,* that *Ctenamphiura* is characterized by its large outer oral papillae which exceed in size the inner papillae. On subsequent study, I found the true relations to be as stated above and as illustrated in Fig. 14—where the infradental papillae have been drawn overturned to show their real size and the peculiar reflexed condition of the true outer papillae indicated.

C. dawbini and the genotype, *C. maxima,* share in common not only the generic characters as defined by Verrill (1899)—that is, the characteristic structure and arrangement of the jaws and accessory plates and oral shields—but also the fact that the arm-spines are arranged to form combs. Since it is obvious that Verrill had these combs in mind when he erected the genus, it seems strange that he omitted to note their presence when defining it; the diagnosis clearly should include the character. The two species agree also in the large size of their tentacle scales and the lumpy character of the disc-plates. *C. dawbini* is distinguished from the congener by having only one (instead of two overlapping) tentacle-scale, and by the partly naked character of the underside; also by the reflexion of the spiniform oral papillae.

Ophiactis Luetken, 1856

Ophiactis resiliens Lyman, 1879

Island Bay Shelf, ca. 100 fathoms, on rock from sea-bed tangled in fisherman's trawl, July, 1950; C. A. Fleming; two specimens.

Ophiactis profundi Ltk. & Mrtsn., 1899

Island Bay Shelf, 100 fathoms (as above); five specimens.

Neither of the above species has spines on the disc; they are separable easily by the fact that the former is regularly five-armed, the latter six-armed, and transversely fissiparous, having usually three large and three small arms.

Ophiocentrus Ljungman, 1867

Ophiocentrus novae-zelandiae Gislen, 1926

Lachlan station 617/50. In bottom-mud off survey-beacon anchor, November, 1950; 40° 15′·0 S., 174° 57′·5 E., ca. 50 fathoms; one specimen.

Family OPHIOCHITONIDAE

Ophionereis Luetken, 1859

Ophionereis novae-zelandiae Mrtsn., 1936

Alert station 19, one specimen.

Island Bay Shelf, ca. 100 fathoms, July, 1950; one specimen.

The disc is grey, the arms grey with narrow black bands at 1 mm. intervals. The coloration is retained but little altered in spirit.

Ophionereis fasciata (Hutton, 1872)

New Golden Hind station NGH L14, one specimen.

Alert stations: 4, one specimen; 13, one specimen; 20, six specimens; 18, one specimen.

H. L. Clark (1928), after examining a good series of the Australian *Ophionereis schayeri* (M. & T., 1844), considers that the differences which Mortensen (1924) found between this and the New Zealand form " . . . are by no means as constant as could be desired . . ." Clark had, however, only a few New Zealand specimens to go upon, and reached no conclusion.

I have examined over the past few years a very extensive series of New Zealand forms from widely scattered localities, including the Auckland Islands, and find that Mortensen's diagnosis of *O. fasciata* holds good. In one specimen from *Alert* station 18, however, although the skeletal characters are normal and the structure of the genital clefts and their relationship to the oral shield and general undersurface is as for *O. fasciata*, the coloration is unlike the usual marbled combination of black, grey, brown, and fawn mottling and banding; instead, there is a greyish-purple disc and arms, lighter below.

Family OPHIOCOMIDAE

Ophiocoma L. Agassiz, 1835

Ophiocoma bollonsi Farquhar, 1908

Alert station 13, two specimens.

East coast of Otago, between Moeraki and Taiaroa, 40 fathoms; P. M. Ralph, November, 1951; four specimens.

Off Banks Peninsula, 80 fathoms, 44° 15′·0 S., 173° 31′·0 E.; coll. G. A. Knox; arm fragments.

The specimens from the stations to the east of the South Island are large ones, the largest having R, 100 mm., r, 14 mm. The colour in all cases is dark brownish-purple. H. L. Clark has treated club-shaped spines in *Ophiocoma* as being of systematic value; however, the presence of three kinds of spines on otherwise similar material from off Banks Peninsula would confirm Mortensen's opinion that club-shaped spines are pathological.

Ophiopteris E. A. Smith 1877

Ophiopteris antipodum E. A. Smith, 1877

Off east Canterbury coast, 40 fathoms; P. M. Ralph; one specimen; see Fell (1951).

Family OPHIODERMATIDAE

Pectinura Forbes, 1843

Pectinura maculata (Verrill, 1869)

New Golden Hind station NGH 57A, one specimen.

Alert stations: 3, one adult; 12, one young specimen; 13, eight young specimens and six half-grown.

Ruapuke oyster beds, Foveaux Strait, 12 fathoms, February, 1951; B. M. Bary; two specimens (extremely abundant).

The young of this large species have not hitherto been recognized; indeed, their colouring and general appearance are so different from that of the adult that, were it not for the taking of a consecutive series of stages, they would not have been recognized on the present occasion. In the stage at which the animal is about two centimetres to four centimetres in diameter, the arms are vermilion and the disc ochre, with a dark orange periphery, orange below. In dissecting a specimen from station 13 (Dusky Sound), I was surprised to find the stomach packed with what appeared to be some kind of flower (the specimen was dredged in 12 to 15 fathoms). Subsequently, Dr. J. G. Gibbs, of Victoria University College Botany Department, identified the material as anthers of Southern Beech, *Nothofagus* sp.

This was later confirmed by Mr. W. F. Harris, of the New Zealand Department of Scientific and Industrial Research; he states: "The pollen was of *Nothofagus*; 52 grains were measured and pore counts were made simultaneously on 26 grains. There were 16 per cent. with seven pores and 84 per cent. with eight pores. The size range was 29μ to 39μ, with an average of 34μ." The ophiuroid had been selectively feeding upon the anthers, since nothing else was in the stomach. This is only the second record to my knowledge of an echinoderm feeding upon terrestrial plant material; the other is the case of a deep-sea echinoid in the East Indies which feeds upon the leaves of dicotyledonous trees washed out to sea by rivers.

Pectinura gracilis Mrtsn., 1924

Alert stations: 2, two large specimens; 3, one specimen; 13, fifteen small individuals; 20, eight specimens; 25, one specimen.

Island Bay Shelf, 100 fathoms, July, 1950; one specimen.

The species is evidently the South Island equivalent of *P. cylindrica*, as no specimens of the latter have ever been reported south of Cook Strait.

Family OPHIOLEPIDIDAE

Ophiozonoida H. L. Clark 1915

Ophiozonoida picta H. L. Clark, 1915

Five miles north of Cape Palliser, February, 1947, coralline bottom, 50 fathoms; F. Abernethy; one specimen.

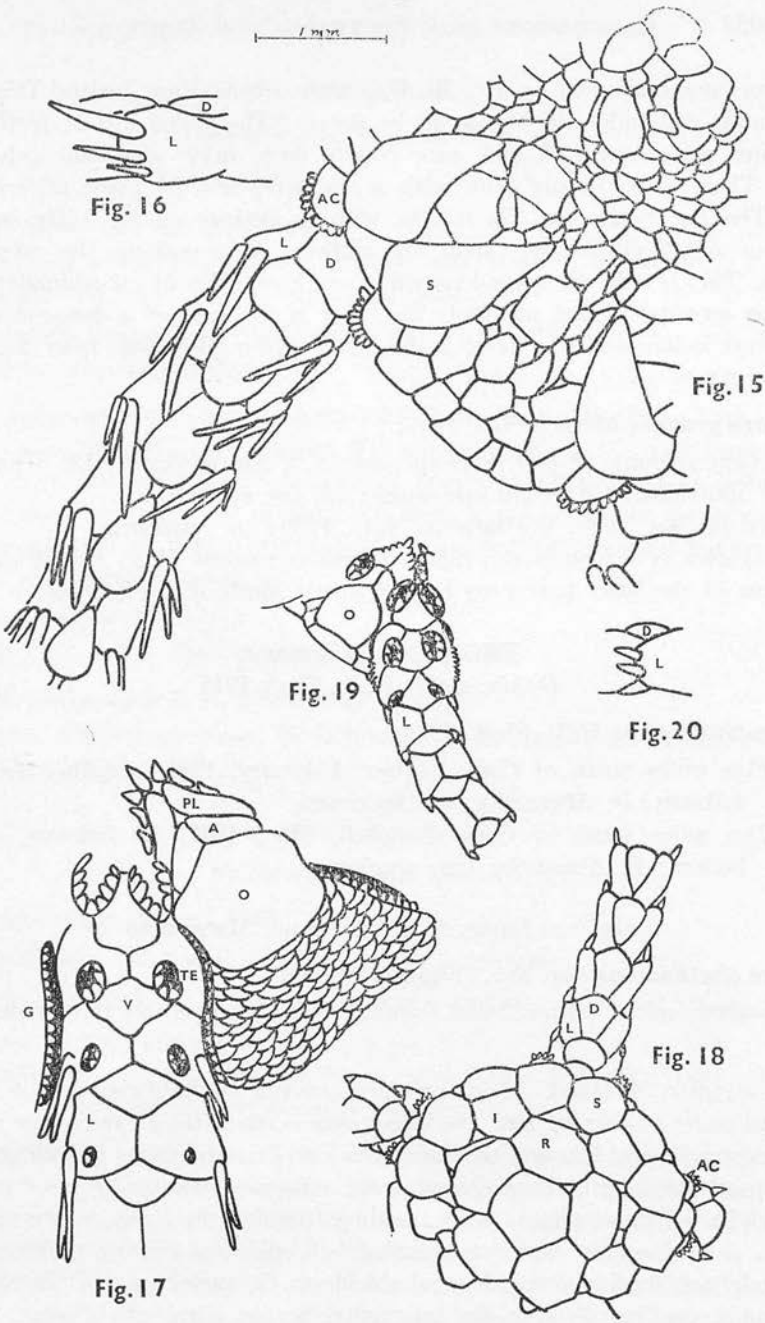
Ten miles south of Cape Campbell, May, 1947, 50 fathoms, coralline bottom; F. Abernethy; one specimen.

Ophiura Lamarck, 1816, emend. Matsumoto

Ophiura chathamensis sp. nov. (Figures 15 to 20)

Dimensions: minor radius, 3 mm.; arms broken, but probably three times minor radius.

Disc, circular, flattened. Aboral surface covered by imbricating, thin, closely adpressed scales of varying size; the larger ones occur at the centre, at the ambitus, in the interradii, and between the radial shields. Primary plates indistinct. Radial shields pearseed-shaped, distally contiguous, separated proximally by a wedge of six or eight polygonal plates, and extending less than half-way to the centre of the disc. Adoral surface completely scaled by closely imbricating uniform plates. Genital clefts extending from the oral shields to the upper part of the arm-base, with genital papillae forming the interradial border. Oral shield large, broadly pentagonal, with a convex distal base, concave sides, and an obtuse proximal angle. Adoral plates small, broader than long, meeting broadly within, contiguous only with the proximal border of the oral shield. Oral plates larger than the adoral plates, with three pairs of oral papillae.



Ophiura chathamensis sp. nov.

Fig. 15.—Aboral view. Fig. 16.—Lateral view of arm-segment. Fig. 17.—Adoral view. Figs. 18 to 20.—Aboral, adoral, lateral views respectively of young individual of *Ophiura* sp., doubtfully referred *O. chathamensis*. All to scale shown.

Abbreviations: A, adoral plate. AC, basal arm-comb. D, upper arm-plate. G, genital cleft. I, primary interradial plate of disc. L, lateral arm-plate. O, oral shield. PL, Oral plate. R, primary radial plate of disc. S, radial shield. TE, tentacle pore, with scales. V, lower arm-plate.

Arms: provided with basal arm-combs, each carrying about ten papillae. Upper arm-plates contiguous on the proximal four segments, thereafter isolated, their shape changing from subquadrate at the base to longitudinally ovate at the fourth plate and beyond, the narrow end of the ovate plates being proximal. Lateral plates meeting both above and below, save on the segments bearing the first four upper arm-plates, where the lateral plates meet below only. They bear three slender, pointed arm-spines, of which the uppermost is longest, equal in length to one segment, the lowermost smallest. Lower arm-plates small, not contiguous, mostly fan-shaped with a proximal obtuse angle and convex distal border; but those of the second and third arm-segments are transversely rhomboid, and that of the first segment longer than broad. Second oral tentacle-pores large, opening into the oral clefts, each ringed by nine or ten small scales. The first three or four lateral plates of the arm carry each a tentacle-pore, the first one large with four or five scales, the second of medium size with three scales, the third (and fourth, if present) minute with one or no scale; beyond, there are no pores.

Colour, in spirit, white.

Type locality: *Discovery* station 2733, Chatham Rise, west of Chatham Islands, 300 metres, November 4, 1950; one specimen.

Holotype: Zoology Museum, Victoria University College.

From *Ophiura rugosa,* the only other species of *Ophiura* known from New Zealand, *O. chathamensis* is sharply distinguished. The former has large, rounded aboral plates arranged in a symmetrical pattern, the proximal under arm-plates are contiguous, and the arm-spines are very short. *O. chathamensis* shares with *Ophiocten hastatum,* a generic relative, the character of having slender spines in groups of three, the uppermost elongate; but it is distinguished by lacking the uniformly fine scaling of the aboral surface and by the larger and differently shaped radial shields. Benham's *Ophiura kermadecensis* is now referred to *Amphiophiura,* and is not similar to the present species.

Of the Pacific species of *Ophiura, O. chathamensis* appears to be more nearly related to *Ophiura ooplax* (H. L. Clark) than to any other—a species which ranges from Japan to South Australia. The resemblance is most marked in the form of the radial shield, the general structure of the arms, and the three slender arm-spines. The differences, however, are considerable: the arm-combs are lost in the adult *O. ooplax,* where, also, all the arm-spines are elongate. In *O. chathamensis,* there are three oral papillae (eight or nine in *O. ooplax*), and the tentacle-pores decrease in size more rapidly than they do in the latter species. *O. chathamensis* also has a finer aboral scaling than *O. ooplax.*

The ophiuroid illustrated (Figs. 18 to 20) was taken with this species at *Discovery* station 2733. Despite the large oral shields, which suggest *Amphiophiura,* it is clearly an *Ophiura,* as the rapid declension of the tentacle-pores indicates. Although the aboral surface of the disc is markedly different, and there are only

two arm-spines, it exhibits considerable resemblance to *O. chathamensis,* of which it might be a juvenile stage. I therefore refrain from doing more than illustrate its structure.

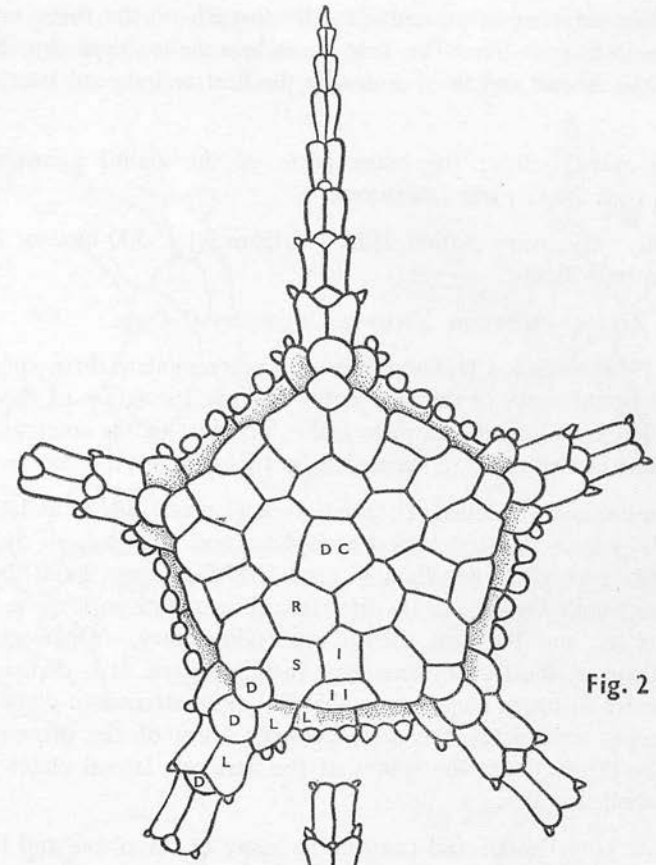
Ophiomisidium Koehler, 1914

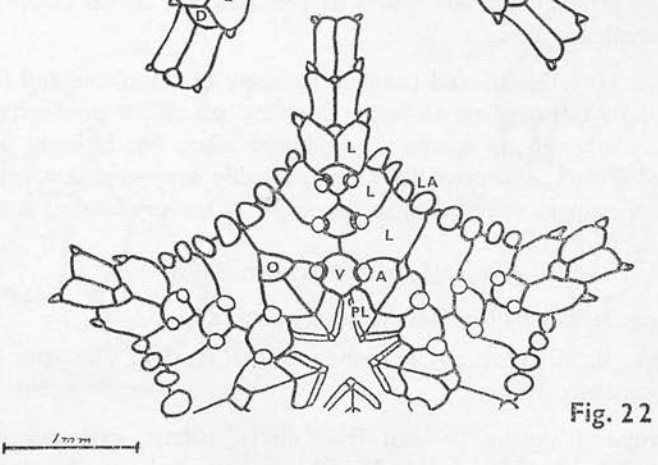
Ophiomisidium irene sp. nov. (Figures 21 and 22)

Dimensions: R, 4·0 mm.; r, 1·5 mm.; ratio R/r, 2·7. The holotype and syntypes are all similar.

Disc: pentagonal, flattened above and below. The aboral surface of the disc is made up of a symmetrical mosaic of 26 plates, all polygonal and interlocking. These comprise the following: At the centre lies the pentagonal dorso-central; it is surrounded by a ring of five hexagonal primary radials; outside these is a ring of fifteen plates, five of them pentagonal primary interradials, the remainder the five pairs of radial shields. The latter are pentagonal and contiguous. A transversely elongate secondary interradial intervenes between adjoining pairs of radial shields. The adoral surface is largely made up of the first lateral arm-plates. The oral shield is vestigial, rhomboid. Adoral plates are longer than broad, contiguous over most of their length, meeting the oral shield only on their distal borders, their lateral borders emarginated by the first large tentacle-pore (whose scale they carry). The oral plates are broader than long, broadly contiguous with each other as well as with the adoral plates. Oral papillae represented only by a narrow marginal bar along each oral plate.

Arms: short, expanded at the base, tapering distally to a slender extremity, nine arm-segments. There are five upper arm-plates; the first fan-shaped, contiguous with the radial shields, and overlapping upon the second; the third, fourth, and fifth also fan-shaped, but not contiguous, and diminishing in size rapidly in that order. Distal arm-segments without upper arm-plates. Lateral arm-plates well developed on all segments, the first far the largest, the second much smaller, the third and succeeding ones tapering more gradually. The first lateral arm-plates of each side are broadly contiguous not only with each other, but also with their corresponding member of the adjoining arm. Hence they form a closed ring completely investing the oral skeleton. They comprise most of the interradial area below, all but obliterate the oral shields, and completely obliterate the genital clefts. The lateral plates meet above and below on all segments except the first, where they meet below only. The first and second lateral plates bear on their free edges two flattened scales, which evidently represent modified spines; the scales form a fringe round the whole disc. The third and fourth lateral plates carry each only one short, stumpy spine, and thereafter there are no more spines. There are five lower arm-plates, the innermost largest, the second and third moderately large, the outer two minute. The first three lower arm-plates are more or less pentagonal, having their lateral borders emarginated by the three large tentacle-





Ophiomisidium irene sp. nov.

Fig. 21.—Aboral view. Fig. 22.—Adoral view.

Abbreviations: A, adoral plate. D, upper arm-plates. DC, dorso-central primary plate of disc. I, primary interradial plate of disc. II, secondary interradial plate of disc. L, lateral arm-plates. LA, spines of basal lateral arm-plate, modified as flattened scales. O, oral shield. PL, oral plate. R, primary radial plate of disc. S, radial shield. V, lower arm-plate.

pores. There is only one large tentacle-scale to each of the three tentacle-pores, flattened, rounded, scale-like. The first tentacle-scale is borne by the adjoining adoral plate, the second and third scales by the first and second lateral arm-plates respectively.

Colour, in spirit, white; the outer parts of the aboral primary plates are porcellanous, their inner parts translucent.

Type locality: *Discovery* station 2733, Chatham Rise, 300 metres, November 4, 1950; sixteen individuals.

Holotype: Zoology Museum, Victoria University College.

Koehler (1914) founded *Ophiomisidium* to accommodate three species specially characterized by the entry of the arm-plates into the formation of the oral surface of the disc. The first lateral arm-plate makes up most of the interradius, the first lower arm-plate is large, and is succeeded by two others not quite so large.

Of the three species included, *O. pulchellum* (Lyman, 1878) and *O. speciosum* Koehler (1914) have the first lateral arm-plates less enlarged, so that the genital clefts are still present. *O. flabellum* (Lyman, 1878), known from the continental shelf off New South Wales, has the first lateral arm-plate so large as to obliterate the genital clefts, and the oral shields are rudimentary. *Ophiomisidium irene* therefore belongs to the *O. flabellum* type in this regard. It is distinguished from the latter species in many respects, notably the more attenuated distal arm region, the larger upper arm-plates, the more compact form of the primary interradial plates, and by the fact that the spines of the first two lateral plates are modified into large rounded scales.

The delicate porcellanous and translucent lustre of the plates and the symmetry of the whole animal combine to make this tiny sea-star a microscopic object of great beauty. Although no species of *Ophiomisidium* has hitherto been taken in New Zealand waters, representatives are probably very common, since no fewer than sixteen specimens were taken in the single *Discovery* haul at station 2733.

Ophiomastus Lyman, 1878

Ophiomastus stellamaris sp. nov. (Figures 23 to 27)

Dimensions: R, 10·0 mm.; r, 1·5 mm.; ratio R/r, 6·7. The arms are relatively shorter in immature forms.

Disc: circular in outline as seen from above, robust, extremely tumid above, so that the profile is semi-circular. Aboral surface completely covered by imbricating scales, of which the six primaries occupy most of the area in the adult (Fig. 23); in the immature form the six primaries comprise the whole of the aboral surface of the disc (Fig. 26). There is a large pentagonal dorso-central, surrounded by the five primary radials which are of irregular polygonal shape in the

adult (though more nearly pentagonal in the young). Beyond these lie five small, irregularly shaped interradials and five pairs of small, polygonal radial shields. Sundry small angular platelets make up the ambital region and fill in the interstices

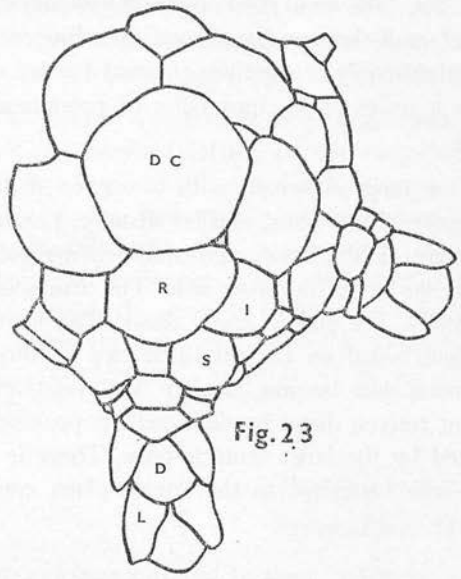


Fig. 23

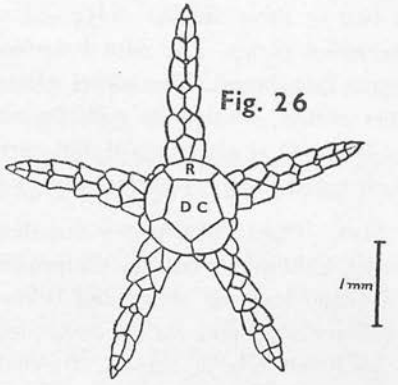


Fig. 26

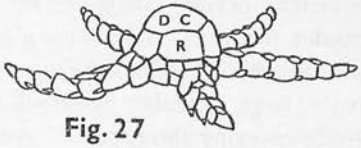


Fig. 27

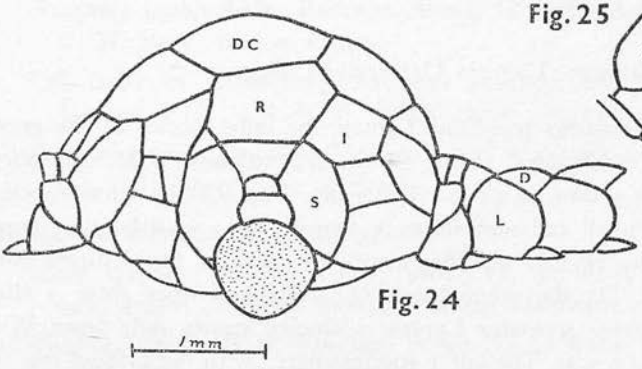


Fig. 24

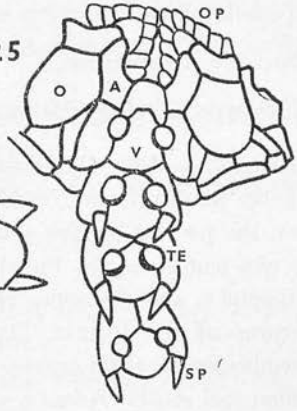


Fig. 25

Ophiomastus stellamaris sp. nov.

Fig. 23.—Aboral view. Fig. 24.—Lateral view of disc and base of arm, seen from radial aspect, to show its hemispherical tumidity. Fig. 25.—Adoral view. Figs. 26 and 27.—Aboral and oblique lateral views of young individual, showing large primary plates.

Figs. 23 to 25 to scale shown below. Figs. 26 and 27 to scale at right.

Abbreviations: A, adoral plate. D, upper arm-plate. DC, primary dorso-central plate of disc. I, primary interradial plate of disc. L, lateral arm-plate. O, oral shield. OP, oral papillae. R, primary radial plate of disc. S, radial shield. SP, spine of lateral arm-plate. TE, tentacle-scale. V, lower arm-plate.

between the larger plates. Usually, but not always, there is a vertical row of several interradial plates (as in Fig. 24). The radial shields are confined to the edge of the disc, at the insertion of the arms, and are separated from each other by two or three smaller polygonal scales, and from neighbouring shields by the interradial plates. The adoral surface is flat. The oral shields are shield-shaped, longer than broad. The adoral plates are small, longer than broad, meeting each other within, contiguous with the oral shields only along the proximal border of the latter. Oral plates small, but carrying a series of ca. four pairs of prominent, quadrangular, closely-packed oral papillae.

Arms: Upper arm-plates fan-shaped, as long as broad, with a convex distal border, contiguous only in the proximal part of the arms, smaller distally. Lateral arm-plates meeting above and below, except on the basal segments, bearing each a solitary arm-spine on the distal, median border of the lower side. The arm-spine is small but robust, conical, directed distally, not visible from above. The lower arm-plates are contiguous and longer than broad on the proximal two or three segments; beyond, they are not contiguous, but become smaller, and relatively broader than long; they have a prominent convex distal border, and the proximal half of each lateral border is emarginated by the large tentacle-pore. There is a single, large, circular, flattened tentacle-scale, attached to the lateral plate, completely covering the pore.

Colour, in spirit, creamy white.

Type locality: *Discovery* station 2733, Chatham Rise, 300 metres, November 4, 1950; eleven specimens.

Holotype: Zoology Museum, Victoria University College.

Remarks.—With *Ophiomastus tegulitius* Lyman, the only species of the genus hitherto known from New Zealand (Cook Strait, 275 fathoms, H.M.S. *Challenger*), the present species shows no close relationship. The slit-like tentacle-pores, the two tentacle-scales (small and semi-lunar in shape), the paired laterally-borne arm-spines, and the more rapidly tapering arms are some of the distinguishing features of the former. On the other hand, *O. stellamaris* does show a close resemblance to *Ophiomastus secundus* Lyman, a species known only from West Indian and central Atlantic seas. The latter species shares with the present one the possession of a single large tentacle-scale, and may have only one arm-spine. However, in *O. secundus*, two arm-spines occur, even in small individuals, and they are carried, furthermore, on the sides of the arm, not below; also, the oral plates do not carry oral papillae, only a marginal border representing them. In most other respects, the two species are quite similar. From *O. perplexus* Koehler and *O. tumidus* Koehler, the species likewise differs in having only one arm-spine.

Class Echinoidea

Family CIDARIDAE

Goniocidaris Agassiz and Desor, 1846

Goniocidaris umbraculum (Hutt., 1872)

East coast of Canterbury, between Moeraki and Timaru, 40 to 60 fathoms, January, 1951; coll. P. M. Ralph; one specimen.

The species is restricted to New Zealand, where it is known only between Cook Strait and Stewart Island, on the eastern coast of the South Island. The single specimen does not differ from Mortensen's account, and is similarly coloured to his specimens. Among the epizoic animals carried on the spines is an acorn-barnacle (*Balanus* sp.), a calcareous sponge, and miscellaneous polyzoa. The majority of the upper spines are completely invested by these organisms. To a lesser extent, the same is to be observed in *Ogmocidaris benhami*, where I have also noted the tubicolous annelid *Spirorbis* attached to the proximal parts of spines; *O. benhami*, however, is as yet unknown from southern New Zealand waters.

Family TEMNOPLEURIDAE

Pseudechinus Mrtsn. 1903

Pseudechinus huttoni Benham, 1908

Station NGH 2; seven tests.

Ruapuke oyster beds, Foveaux Strait, 12 fathoms, February, 1951; coll. B. M. Bary; two specimens.

Off coast of Canterbury, between Moeraki and Timaru, 40 fathoms, January, 1951; coll. P. M. Ralph; three specimens.

Off Otago coast, between Moeraki and Taiaroa Head, 40 fathoms, November, 1951; three large specimens.

Pseudechinus albocinctus (Hutton, 1872)

Alert stations: 11, three dead tests; 13, ten dead tests of very young individuals; 23, three immature living specimens.

Ruapuke oyster beds, Foveaux Strait, 12 fathoms, February, 1951; coll. B. M. Bary and C. A. Fleming; three specimens.

Off Otago and Canterbury coasts, between Taiaroa Head and Timaru, 40 fathoms, January and November, 1951; coll. P. M. Ralph; six specimens.

Pseudechinus novae-zelandiae (Mrtsn., 1921)

Alert stations: 11, two dead tests of young individuals; 13, five young dead tests; 23, five young living specimens; 24, one young specimen.

Ruapuke oyster beds, Foveaux Strait, 12 fathoms, February, 1951; B. M. Bary; one specimen.

Off East Canterbury coast, between Timaru and Moeraki, 40 fathoms, November, 1951; P. M. Ralph; two large specimens.

It would appear that in the southern part of New Zealand the three species of *Pseudechinus* occur side by side. In the material examined, it was notable that wherever specimens were taken in either young or old stages, large forms or small, dead or living, the particular character, whatever it might be, applied pretty well equally to all three species. A consistently small size of individuals from the Fiords is notably in contrast with an equally consistent occurrence of large specimens off the east coast of the South Island. In both the *New Golden Hind* and the *Alert* dredgings, there was a surprising preponderance of dead tests of immature and even post-embryonic individuals in the Fiords region. Some had annelid tubes or small corals growing on them. The reason for this is not clear. Some specimens, especially from station NGH 2, had adhering mud, as if from a soft bottom—a habitat not frequented by *Pseudechinus*. On the other hand, Mr. C. A. Fleming, of the New Zealand Geological Survey, informs me (private communication, 1952) that the mollusca from the same station indicate a hard bottom, though the species present are few. It is possible that there are rapid transitions from hard to soft bottom in the Fiords, and that mud frequently overwhelms the hard-bottom communities. Fleming has found analogous sequences in the Castlecliffian strata (Upper Pliocene), hard and soft-bottom communities alternating. This probably accounts for the presence in the Castlecliffian of *Pseudechinus* in mud marl, a matrix not otherwise to be expected for the genus; the Castlecliffian specimens are small, like those from the Fiords.

Family ECHINOMETRIDAE

Evechinus Verrill, 1871

Evechinus chloroticus (Valenciennes, 1846)

Alert station 11, fragments of the test of a large individual.

Also, Dusky Sound, littoral, one large test washed ashore.

The absence of the species from other stations is accountable by the fact of its being especially a reef-dwelling, eulittoral form. It is seldom found fossil for the same reason. It has not hitherto been taken from 50 fathoms (as at *Alert* station 11); but, as fragments alone were found there, the record should not be treated as evidence that the species lives in such deep water.

Family ECHINOBRISSIDAE

Apatopygus Hawkins, 1920

Apatopygus recens (M. Edwards, 1836)

Station NGH 2, a single test of a small individual, bearing tubicolous annelids and coral.

Ruapuke oyster beds, Foveaux Strait, 12 fathoms, February, 1951; B. M. Bary; two specimens; also from the same locality, one specimen; coll. C. A. Fleming.

Off Chatham Islands, taken from stomachs of groper (*Polyprion oxygeneios*); coll. F. Abernethy; numerous specimens.

Family LAGANIDAE

Peronella Gray, 1855

Peronella hinemoae Mrtsn., 1921

Station NGH 3, one specimen.

Alert stations: 13, four dead tests; 18, three dead tests.

These records extend the range of *Peronella hinemoae* southward by over 700 miles; it has hitherto been known only from Hauraki Gulf, Colville Channel, and North Cape. The largest specimen measures 40 mm. horizontal diameter. The records also indicate a shallower habitat than formerly was known.

Family SPATANGIDAE

Spatangus Mueller, 1776

Spatangus multispinus Mrtsn., 1925

Cape Campbell, 20 fathoms, soft mud bottom, September, 1949; one specimen.

In life, the species is bright purple, fading after preservation to dull mauve. It is known so far only from the Cape Campbell area.

Echinocardium Gray, 1825

Echinocardium cordatum (Pennant, 1777)

Synonym: *Echinocardium australe* Gray, 1851, *et auctt.*

New Golden Hind stations: NGH 1, two specimens; NGH 3, three specimens; NGH 56A, two specimens.

Alert stations: 1, one specimen, not common; 3, two specimens, but very abundant; 4, one specimen, not common; 6, one specimen, not common; 10, one specimen, but abundant here; 12, one specimen, not common; 19, eight specimens, one very large; 29, two specimens, abundant.

Also, near entrance to Queen Charlotte Sound, 20 to 30 fathoms, May, 1950; W. H. Dawbin; one specimen.

The large specimen from *Alert* station 19 (Stewart Island) measures as follows: Length, 69 mm.; breadth, 66 mm.; height, 38 mm.

H. L. Clark (1946), who has taken the step of merging the Australian *Echinocardium australe* with the Atlantic species *E. cordatum*, states that specimens from the southern hemisphere attain only about half the size of those from Great Britain, rarely exceeding 45 mm. in length. The above record shows that large forms do occur. Mortensen (1921) considers the New Zealand and Australian forms to be identical, and so, in view of the change in nomenclature in Australia, it seems desirable to follow suit in New Zealand.

That the species occurs in Chalky Inlet was shown by Farquhar in 1898.

Class **Crinodea**

Comanthus A. H. Clark, 1908

Comanthus benhami A. H. Clark, 1918

Alert stations: 12, three specimens; 32, six specimens.

Observations and colour sketches from life by Mr. W. H. Dawbin record that the feather-star is a chocolate-purple, swims freely, and specimens attach themselves by their cirri to the outside of the dredge-sack. The specimens of both stations are from Doubtful Sound, and were taken nowhere else. The largest measures: R, 145 mm. This is the second record of the species, which is known only from the Southern Fiords.

COMATULIDAE gen. et sp. indet.—a single specimen from *Alert* station 11, which has been referred to Dr. A. H. Clark for study.

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A Revision of the Current Theory of Echinoderm Embryology.

By

H. BARRACLOUGH FELL,
M.Sc., Ph.D.

Transactions of the Royal Society of New Zealand, Vol. 75, Part 2, pp. 73–101. 27 Figs.

A Revision of the Current Theory of Echinoderm Embryology.

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(Communicated by Professor L. R. Richardson.)

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Introduction.

In October, 1846, Johannes Müller astonished the scientific world of his day by his discovery that a peculiar free-swimming marine animal which he had previously named *Pluteus paradoxus* was in reality the larval stage of an ophiuroid. This was the first demonstration that echinoderms undergo an indirect process of development, and the remarkable fact emerging from the observation was that these bottom-dwelling, radially symmetrical animals pass through a stage in their life-history in which they are free-swimming and bilaterally symmetrical. Müller's discovery, and his later researches in the development of the echinoderm groups, were destined afterwards to exert a great influence upon theories as to the origin and evolution of the echinoderms; but their immediate effect was mainly upon the science of embryology, stimulating research workers to identify and elucidate other free-swimming larval forms.

The subsequent history of echinoderm embryology is too complex to be capable of summary here, but in its main lines it can be expressed in a single statement. It has resolved itself into the simple and dogmatic doctrine that all typical echinoderms pass through a free-swimming larval stage. There are various adjuncts to this doctrine, the most notable being the widely accepted statement that the coelom of echinoderms is always an enterocoel. This paper is concerned with a critical examination of the evidence upon which the doctrine is based.

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The Problem.

The problem under consideration may be briefly enunciated—"To what extent does direct development occur in echinoderms; what are its causes; by what processes does it take place; and what evidence does it provide of the evolutionary history of the echinoderms?"

In view of the more extensive nature of our knowledge of the subject in the Ophiuroidea, the present paper is predominantly concerned with that class, but wherever material is available comparisons are made with conditions holding in the other classes.

Material for Evidence.

The evidence upon which this investigation is based is as follows:—

(a) Our previous knowledge of the indirect, pelagic type of development. This is founded mainly on the researches of MacBride (1907) on *Ophiothrix fragilis* and the recent work of Narasimhamurti (1933) on *Ophiocomina nigra*.

(b) Our previous knowledge of the development of a moderately yolky ophiuroid egg. This is founded solely on Grave's work on *Ophiura brevispina* (1900 and 1916).

(c) The recently published work of the writer on Kirk's ophiuroid, a form with very yolky eggs, and on *Ophiomyxa brevirima*, a viviparous form also with very yolky eggs (1940 a, 1941).

(d) The scattered body of data in the literature in regard to isolated stages of development of other ophiuroids—mainly referring to larval forms.

(e) The research presented elsewhere (Fell, 1945) on *Amphipholis squamata*, a form with moderately yolky eggs and of viviparous habit.

It will be seen from the above list that there is a fairly representative body of data available, ranging from non-yolky eggs to those with a very large proportion of yolk, and including cases of viviparity. In addition to these data, there is a considerable amount of scattered information on the other echinoderm classes, but in no case presenting so complete a sequence as is now available from the Ophiuroidea.

The method adopted in this investigation is comparative and analytical—i.e., each of the principle phases of development is taken separately, and examined with reference to the forms showing indirect development, those showing intermediate characters, and those showing direct development.

What is the "Typical" Echinoderm Development?

Before commencing the study of the nature of direct development in echinoderms, it will be useful to examine the position in regard to development in general in this group. As pointed out in the introductory section of this paper, it has come to be generally assumed that all "typical" echinoderms have an indirect development; consequently, whenever an echinoderm has been found which departs from this criterion, it has been glossed over in the text-

books with a remark to the effect that it is "not typical"—and hence unworthy of further consideration.

Examples of this attitude are abundant. Thus, commenting on the development of *Antedon*, MacBride (1914) states, "We may discount the characteristic features of the development of *Antedon*, which are obviously due to the yolky egg . . .", etc. *Antedon*, it should be noted, is the *only* crinoid of which we have any embryological knowledge, yet, because it lacks a larva comparable to the Ophiopluteus or Bipinnaria it is automatically rejected as "atypical," for, it is stated, a "typical" crinoid must undoubtedly possess a bilaterally symmetrical and non-yolky larva.

If echinoderms with yolky eggs—and consequently having direct development to a greater or less degree—are held to be atypical, then obviously a census of the echinoderms of whose development we have any evidence should reveal at once that directly developing forms constitute the great minority. It should be found that most echinoderms have an indirect development, coupled with a pronounced larval stage. Is this the true position? In order to obtain some information on this question I have selected three specimen faunas for special examination. These are the echinoderm faunas of Great Britain, of New Zealand, and of the Antarctic and Sub-Antarctic. In these we may expect to find reasonably typical samples of the world's echinoderms.

British Echinoderms.

A survey of the literature shows that there are some 61 British echinoderms about which we have sufficient information to be able to deduce with a fair degree of certainty the type of development which they follow. This is a larger proportion of the entire fauna than holds in other regions, and is attributable to the fact that most British species are found over a large part of the northern European seas, where most research work on the subject has been done. Taking first those species whose development is either known to be shortened, or which may be regarded as fairly certain to be so, we have the following list:—

Holothuroidea. (Seven species.)

Mesothuria intestinalis
Bathyplotes natans
Cucumaria frondosa
Cucumaria planci
Psolus phantapus
Leptosynapta minuta
Labidoplax buski

Crinoidea. (Two species.)

Antedon bifida
Antedon petasus

Asteroidea. (Twelve species.)

Ctenodiscus crispatus
Psilaster andromeda
Pontaster tenuispinus
Ceramaster granulatus
Hippasterias phrygiana
Asterina gibbosa
Solaster papposus
Solaster endeca
Henricia sanguinolenta
Brisingella coronata
Leptasterias mulleri
Pedicellaster typicus

Ophiuroidea. (Four species.)

Asteronyx loveni
Ophiomitrella clavigera
Ophiopus arcticus
Amphipholis squamata

Echinoidea. (Two species.)

Poriocidaris purpurata
Neolampas rostellata

NOTE.—The larvae of *Amphiura filiformis* and of *Ophiura affinis*, although pelagic, lack the full development, and may be regarded as representing stages in the adoption of a shortened development, in addition to the four ophiuroids named above.

Taking now those species whose development is either known or believed to be of the indirect or pelagic type, we have the following:—

Holothuroidea. (Three species.)

Stichopus tremulus
Holothuria forskali
Labidoplax digitata

NOTE.—Only one Auricularian larva has been taken in British waters—that of *L. digitata.*

Crinoidea.

None.

Asteroidea. (Seven species.)

Astropecten irregularis
Luidia sarsi
Porania pulvillus
Stichastrella rosea
Asterias rubens
Marthasterias glacialis
Pedicellaster sex-radiatus

Ophiuroidea. (Twelve species.)

Ophiothrix fragilis
Ophiocomina nigra
Ophiactis balli
Ophiopholis aculeata
Amphiura chiajei
Amphiura filiformis
Ophiura texturata
Ophiura sarsi
Ophiura albida
Ophiura carnea
Ophiura affinis
Ophiocten sericeum

Echinoidea. (Twelve species.)

Cidaris cidaris
Psammechinus miliaris
Echinus esculentus
Echinus acutus
Paracentrotus lividus
Sphaerechinus granularis
Strongylocentrotus drobachiensis
Echinocyamus pusillus
Brisaster fragilis
Spatangus purpureus
Echinocardium cordatum
Brissopsis lyrifera

ANALYSIS.

Of ten holothurians about whose development we have any knowledge, only three form Auriculariae. The other seven species all have large yolky eggs and a more or less direct development. Two of these are known to have the special simplified "yolk-larva" which I have termed "Vitellaria" (see a later section of this paper) and the remainder may have absolutely direct devlopment.

Of the two crinoids whose development is known, both have large yolky eggs, and both form the same yolk-larva or Vitellaria.

Among the asteroids, only seven out of nineteen species have a pelagic development. The remaining twelve species all have large yolky eggs and probably direct development to a greater or less extent. In this class there is as yet no evidence of the existence of the "Vitellaria" larva.

In the ophiuroids, of the sixteen species about which there is any evidence, four have direct development as a result of viviparity or large yolky eggs. Of the remaining twelve species, not all have typical plutei, and stages in the loss of the arms are to be observed. In a species of *Ophiura* a Vitellaria is known.

In the echinoids there is far less tendency to have direct development. However, of fourteen species about which we have any informa-

tion, two at least have large, yolky eggs and probable direct development. This development is likely to be of the type seen in *Toxocidaris erythrogrammus* of New South Wales. The remaining twelve species have pelagic plutei and indirect development.

Summarising these results, we find that in those British echinoderms whose development is known either in whole or in part, or about which there is any evidence, the following table may be drawn up:—

TABLE I.

Group.	P.c. With Direct Development.	P.c. With Pelagic Unshortened Development.
Holothuroidea	70%	30%
Crinoidea	100%	—
Asteroidea	63%	37%
Ophiuroidea	25%	75%
Echinoidea	14%	86%

From this it is clear that the notion that echinoderms are typified by having an indirect development with pelagic larvae is without foundation. The theory probably originated from the fact that most laboratory work has been done upon the eggs and larvae of echinoids, which, as shown above, are alone notable for tending to have pelagic larvae.

NEW ZEALAND ECHINODERMS.

Turning now to the New Zealand echinoderm fauna, I select the ophiuroids for particular mention, as I have had opportunities for personal study of these forms in recent years.

Mortensen showed in 1924 that at least six New Zealand ophiuroids are viviparous. All of these lack a free-swimming larva and have a more or less direct development. In the case of *Ophiomyxa brevirima* direct evidence has been produced that this is so (Fell, 1940 a). In addition it has been shown that the oviparous form known as "Kirk's ophiuroid" has an absolutely direct development. I have also described the large, yolky egg of *Pectinura maculata* which indicates a direct development (1941). Other species provide some indication as to the nature of their development from the size of their eggs (see section of this paper on the egg).

The following ophiuroids are known, or are believed to have direct development:—

Ophiomyxa brevirima
Amphiura magellanica
Amphiura annulifera
Amphiura praefecta
Amphipholis squamata
Pectinura cylindrica
Pectinura gracilis
Pectinura maculata
Amphiocnida pilosa
Amphioplus basilicus
Kirk's ophiuroid
Ophiozonoida picta

In addition Mortensen (1924) has given reasons for believing that *Amphiura hinemoae* may have direct or shortened development.

New Zealand ophiuroids whose development is known or believed to be of the indirect pelagic type are:—

Ophiocoma bollonsi
Ophiactis resilicns
Amphiura spinipes
Amphiura rosea
Amphiura amokurae
Amphiura alba
Ophionereis fasciata

The development of the remaining twenty-three species is unknown.

The above tables show that out of nineteen ophiuroids of New Zealand of whose development we have any knowledge at all, twelve—i.e., 63%, are believed to have direct development, and only seven, or 37%, to have indirect pelagic development. Thus, the proportion of ophiuroids believed to have direct development is much higher in New Zealand waters than in those of Britain (and Europe).

Antarctic and Sub-Antarctic Ophiuroids.

Owing to the painstaking work of Mortensen (1936) in his description of the ophiuroids collected by the *Discovery* Expedition, we now have some knowledge of the breeding habits of many southern species, together with information in regard to the eggs. His researches have revealed that out of 56 ophiuroids from this region whose sexual character is known, no less than 31 are viviparous. This high proportion seems to be characteristic of southern seas, as it is not paralleled in Arctic forms.

These 31 ophiuroids must all have more or less shortened developments, without free larval stages. Details have been given above of species from Britain and New Zealand, and there is no occasion to quote any further lists of species here. The reader is referred to Mortensen's paper (1936). However, besides the 31 viviparous forms it appears that some eight species at least have large, yolky eggs and therefore probable direct development. Thus out of the 56 Antarctic species of whose development we have any information, it is highly probable that 39 species, or 70%, have direct development. Of the remainder, only in nine species has it been shown that there is likely to be a pelagic larval stage. Our knowledge of these southern forms must of necessity remain incomplete for a long time, but sufficient is known to show that the majority of them are likely to have direct development.

Conclusions.

No doubt similar evidence of this kind could be provided for the echinoderm faunas of the rest of the world—with the possible exception of the tropical regions, where larval forms of all kinds tend to become exaggerated—but sufficient facts have been given to show that the supposition that a pelagic larval development is "typical" of echinoderms is founded on no evidence whatever. The fact is that no particular kind of development is "typical" for echinoderms in general, but that the kind of development followed depends on the particular conditions obtaining in each species. That these conditions can be analysed and classified will be shown in this paper.

The Phases of Development Analysed.

1. The Ovum.

In the characters of the ovum I believe that we have the clue to the factors controlling development in both the directly developing and indirectly developing forms. These factors can, I believe, be further traced to the cytoplasm of the ovum. But before proceeding to examine the evidence provided by the internal structure of the egg-cell, it will be useful to consider the egg-cell phase as a whole,

TABLE II.

The Inter-relationship Between Egg-size and Mode of Development in Ophiuroids.

Representative Species	Diameter of egg	Group Characteristics
Ophiothrix fragilis *Ophiocomina nigra*	Up to 100 μ	*Group 1.*—Small eggs, long indirect development, with pelagic Ophioplutei.
Amphipholis squamata *Ophiura brevispina*	From 100 μ to 300 μ	*Group 2.*—Eggs of intermediate size, having a shortened development, and with reduced larvae.
Ophiopus arcticus Kirk's Ophiuroid *Ophiomyxa brevirima*	From 400 μ to 650 μ	*Group 3.*—Eggs comparatively very large, with development so shortened as to be direct, without trace of a larval stage.

If we take a series of ophiuroids ranging from forms with indirect, larval development to those with direct, non-larval development, and place their eggs in order of increasing volume, a remarkable fact at once becomes obvious (see Table II). It is found that the eggs of small volume fall into a group the common character of which is the possession of a long period of indirect development involving a pelagic Ophiopluteus stage and metamorphosis. The largest eggs form another group whose common character is the absence of indirect development, the loss of the larval stage, and no metamorphosis. Eggs of intermediate size form a third category exhibiting intermediate stages in the suppression of the larval development. This we can express as a simple and fundamental principle—"*The degree of larval development of an embryo varies indirectly as the volume of the egg from which the embryo is derived.*" Grave (1916) anticipated this "law," but as no cases of completely direct development were known at that time, and the development of only two ophiuroids had been worked out, he was unable to express the fact in a full or convincing manner. His work will be further considered below.

The same relationship between egg-size and development appears to hold good in the other four classes of living echinoderms, but in no case is there as yet so complete a series as is now known from the Ophiuroidea.

In my previous paper on the development of Kirk's ophiuroid (1941) it was suggested that the immediate ontogenetic factor causing the direct development and unexpected method of development of the organs might be the presence of yolk material in the tissues of the developing embryo. The yolk material, it was suggested, might act as a retarding agent, being inert and lifeless. This interpretation of the effect of yolk material accords well with the facts revealed by the sequence of egg types shown in Table II, for in all the cases it is the larger eggs—and consequently those with the greater amount of nutritive material—which have direct development.

In the literature it has been customary to speak of eggs as being " yolky " or " very yolky " or " not yolky "—a method of description which is necessarily inexact. It seemed to the writer that a more precise definition of these arbitrary terms would be of use in determining more accurately the influence exerted by the yolk. Accordingly the following method of quantitative estimation of yolk content in minute eggs was devised, and proved susceptible to mathematical treatment. Sections of known thickness were cut through the egg of an ophiuroid whose yolk content it was desired to estimate. Haematoxylin was used to stain the yolk granules deep black. Then, by using a squared eyepiece the average number of granules in an area of known size was found. Knowing the thickness of the section, it was then possible to calculate the number of granules in a given volume of egg. Next the average diameter of the yolk granules was estimated, and, combining this result with the former, it was possible to estimate approximately the actual volume of yolk material in a given volume of egg. In practice the yolk was estimated as a percentage of 100 cubic microns of egg material. Knowing the average diameter of the egg, it was then possible to determine the absolute volume of yolk material present in the entire egg.

A calculation made in this way shows that in Kirk's ophiuroid there exists in the egg approximately $5{\cdot}3 \times 10^6$ cubic microns of yolk material.

A similar estimation for *Amphipholis squamata*, a form with only " moderately yolky " eggs, yields a figure of circ. $8{\cdot}8 \times 10^4$ cub. μ. Thus we have a much more clear-cut picture of the relative " yolkiness " of these two types of egg, and can now proceed to compare the yolk value with the other variables.

Tabulating the yolk value against the diameter of the egg, as in Table III, it is seen that in these examples yolk content increases with size of egg. This, of course, was merely what has usually been assumed hitherto, though without actual demonstration.

TABLE III.

	Species	
	Amphipholis squamata	Kirk's ophiuroid
Diameter of egg.	100 μ	500 μ
Volume of yolk in egg.	8.8×10^4 cub. μ	5.3×10^6 cub. μ
Cytoplasm expressed as percentage of egg volume.	83%	92%

Having noted that the yolk increases with increasing diameter of the egg, we can now consider the case in regard to the cytoplasm. In this matter the literature provides no information. The tendency, however, has been to suppose that in large, yolky eggs the cytoplasm becomes proportionately reduced, remaining more or less constant in amount while the yolk increases. This attitude is maintained by Grave (1916) who also states that it is impossible to measure the ratio of yolk to cytoplasm. In his latter statement he is, of course,

incorrect, since it is possible to make such measurements by the method described above. In the calculation illustrated, at the stage when the yolk-volume per 100 cubic microns was estimated, the resultant is also automatically an expression of the percentage content of yolk of the whole egg. By a simple subtraction, therefore, we obtain an expression of the percentage content of cytoplasm—ignoring the nucleus in both measurements. Taking now the cytoplasm value as a percentage of egg-volume, it is clear from Table III that comparatively little change in the ratio of cytoplasm to yolk has taken place in the transition from smaller egg-size to larger. This means that as the amount of yolk has increased, so also has the amount of cytoplasm, keeping pace each with the other. The older vague methods of describing "yolky" and "less yolky" eggs failed to bring out this fact, and hence the mistaken notion that the yolk increased and not the cytoplasm. It is therefore necessary to modify the conclusion expressed in my earlier paper on Kirk's ophiuroid (1941) in regard to the influence of increasing yolk-mass, by adding that the effect is associated with a parallel increase in the cytoplasm.

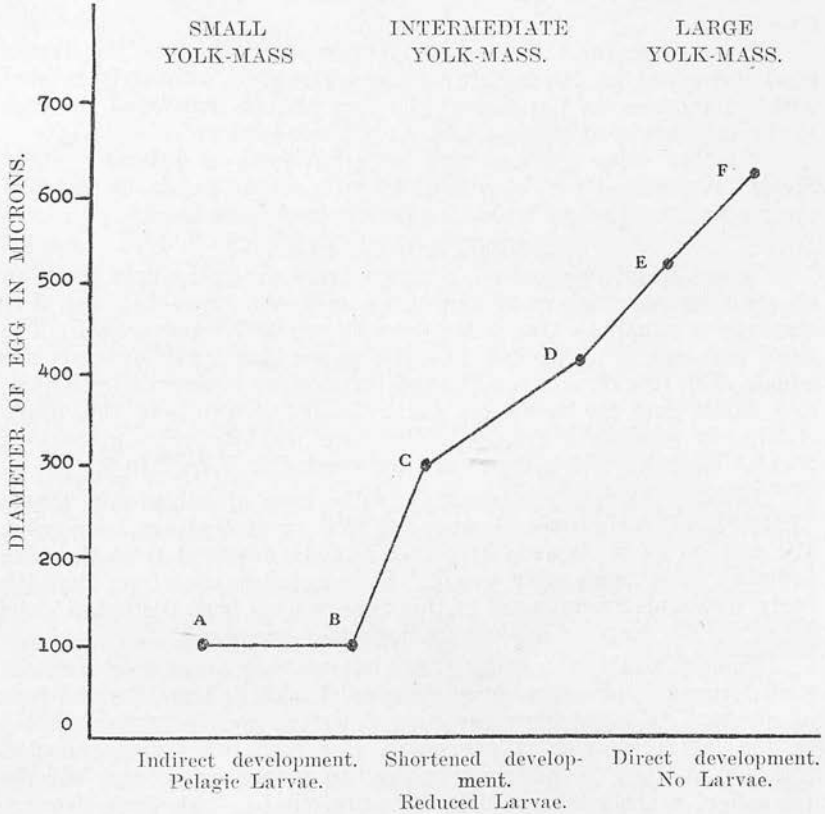


FIG. 1.—Graph showing interrelationship between size of egg, amount of yolk, and type of development in the Ophiuroidea. A, *Ophiothrix fragilis* and *Ophiocomina nigra*; B, *Amphipholis squamata*.; C, *Ophiura brevispina*; D, *Ophiopus arcticus*; E, Kirk's Ophiuroid; F, *Ophiomyxa brevirima*.

Finally, if we combine into one diagrammatic graph the three associated conditions we have been considering in this section of the paper—namely, increasing egg size, increasing yolk content, and shortening of the development—we obtain a convincing demonstration of how the different types of development are interrelated (see Fig. 1). This graph shows that at one end of the scale we have such types as *Ophiothrix fragilis* and *Ophiocomina nigra*, with small eggs and small amount of yolk material. Next comes the group with an increase in the amount of yolk, together with a shortening in the development. This group includes *Amphipholis squamata* and *Ophiura brevispina*. In the case of the latter species, the increase in yolk is associated with increase in egg-size, together with more marked shortening of the development. At the other end of the scale comes the group in which a very much greater increase in yolk material has occurred, together with cytoplasm increase, the eggs have become progressively larger, and the development so shortened as to be direct. In this group are such species as *Ophiopus arcticus*, Kirk's ophiuroid, *Ophiomyxa brevirima* and (probably) *Pectinura maculata*.

Conclusions.

From these facts it is reasonable to conclude that the factor most important in causing direct development is intimately related with an increase in the size of the egg and an associated increase in the amounts of cytoplasm, and its product—the yolk.

Whether other factors may have operated in bringing about direct development will be considered later in the paper, as also will the mechanism through which the factors may have acted.

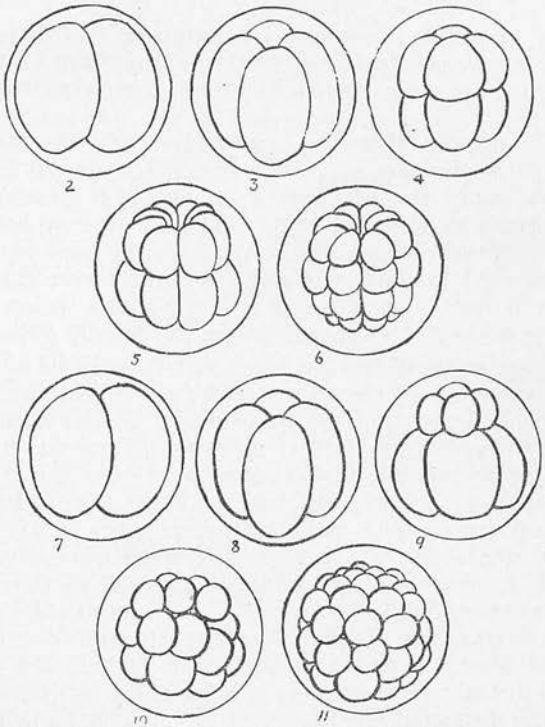
2. The Early Cleavages.

In ophiuroids with small, comparatively non-yolky eggs the plan of cleavage followed is of the usual echinoid type—i.e., the first cleavage is equal, as also is the second, and both are vertical. The third cleavage is horizontal, and the upper and lower quartets are equal. The fourth cleavage is again vertical and more or less equal, and after that the cleavages occur fairly evenly over the whole embryo to produce a morula. The latter rapidly gives place to a regular blastula. These stages are represented in Figs. 2 to 6.

In the case of the moderately yolky eggs of ophiuroids, Grave (1916) has described the cleavages of the egg of *Ophiura brevispina*. His account shows that no difference is to be observed from the plan followed in the non-yolky group. He concludes, therefore, that the early stages of development in this species have been disturbed little if any by the increase in the yolk mass that has occurred.

Coming now to the yolky group having very large eggs, we have such forms as *Ophiomyxa brevirima* and Kirk's ophiuroid. The type of cleavage followed here has been described by the writer (1941) in the latter species. Cleavage in this case follows a somewhat different pattern to that seen in the two preceding groups, but the alteration nevertheless is not very profound. The first cleavage (Fig. 7) is unaltered.* The same applies to the second cleavage

* In about 30% of cases, however, an abnormal cleavage occurred in which the first two blastomeres were unequal, the larger undergoing two divisions to form a normal four-cell stage.



FIGS. 2–11.—Diagrams illustrating the effect of increasing yolk mass on the cleavage of the egg.
FIGS. 2–6.—Cleavage in ophiuroids with small or moderate yolk mass (e.g., *Ophiothrix*, *Ophiocomina*, *Ophiura*).
FIGS. 7–11.—Corresponding stages in cleavage of Kirk's ophiuroid, which has heavily yolked eggs.

(see Fig. 8). When, however, the third cleavage is reached, two quartets are formed which show a marked differentiation into micromeres and macromeres (Fig. 9). This fact indicates that a prelocalisation must have occurred during the four-cell stage, or even earlier. As shown in my paper (1941), the macromeres are destined to form mes-endoderm, and are ventral (aboral) in position. The micromeres form the ectoderm and its derivatives, and in addition contribute to the mes-endoderm. This will be further discussed in the section of this paper dealing with gastrulation. In the cleavage immediately following the third, the division of the blastomeres becomes irregular and " out of step ". Finally, a morula with very turgid blastomeres is formed (see Fig. 11).

The changes to be observed in the plan of cleavage of this very yolky form are undoubtedly to be correlated with the great increase in the yolk material. It is interesting to note that, despite the comparatively enormous quantity of yolk present in Kirk's ophiuroid as compared with *Ophiothrix* or *Ophiocomina*, the plan of segmentation is really but slightly altered. One might, for instance, have expected to find some tendency to adopt partial cleavage, or to form a blastoderm, as has occurred in other groups where increase in the

yolk mass has occurred. Indeed, such a supposition was put forward by Dr. Th. Mortensen in a private communication to the writer; but so far no evidence of such alteration in development has been found.

It would appear that the reason for this retention of the primitive type of division may be correlated with the fact already shown in this paper that the cytoplasm mass has increased in step with the increase in the yolk mass. Again, we may consider that the earliest stages of development are always the most rigid, and the last to be affected by factors producing ontogenetic change. This seems to be indisputable, for, as will be shown below, the later stages come to be tremendously altered in the heavily yolked forms.

One further effect of the increased yolk-mass in Kirk's ophiuroid remains to be noted. This concerns the alteration in the rate of cleavage. In my account of the development of this species, a table was given showing the progress of cleavage during the first twenty-three hours following the first cleavage. From this it was clear that a pronounced retardation had occurred, for whereas other ophiuroids with non-yolky or moderately yolky eggs reach the blastula stage at the end of the first 24 hours, Kirk's form is at that time only at the morula stage. Not till the end of the second day is the blastula completely formed, while the gastrula stage cannot be regarded as complete till the fifth day. On the other hand, other ophiuroids (*Ophiothrix* and *Ophiura*) have formed the gastrula at the thirty-sixth hour. *Ophiocomina*, as described by Narasimhamurti (1933) is slightly slower, forming the gastrula at from the fortieth to the forty-eighth hour.

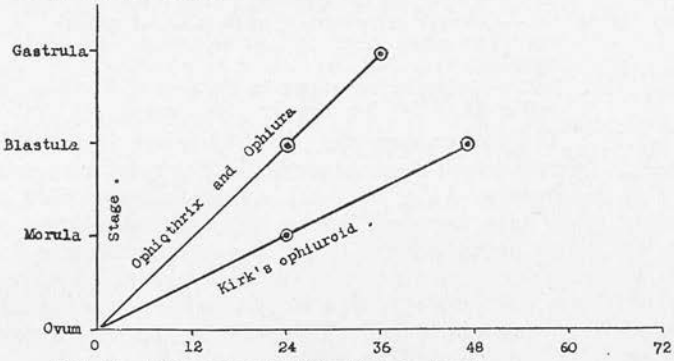


FIG. 12.—Time after fertilisation, in hours.

This retardation is illustrated in graphical form in Fig. 12. As the alteration in developmental rate is associated with increase in the yolk-mass, we can justifiably correlate the two conditions. That the presence of a large quantity of inert nutritive material should have such a delaying action on the ontogenetic processes is not surprising.

3. The Blastula.

Passing now to the blastula stage, we begin to find that changes in the developmental sequence become more pronounced, and furthermore, these changes not only affect the heavily yolked eggs, but become extended to the moderately yolked type.

In the non-yolky type, exemplified by *Ophiothrix*, MacBride (1907) states that there is a free-swimming blastula with ciliated cells. These form a cell-layer one-deep and surround the large, central blastocoel. From the vegetal pole mesenchyme cells are budded off (see Fig. 13).

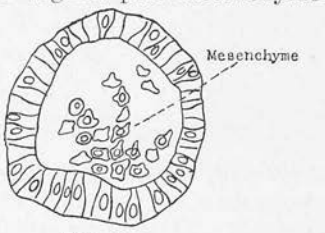


Fig. 13.

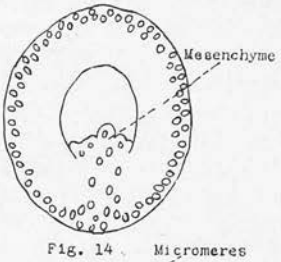


Fig. 14.

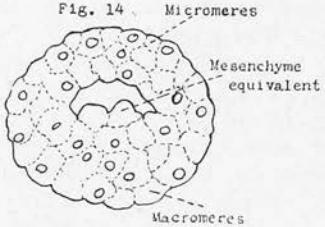


Fig. 15.

FIGS. 13–15.—Diagrams illustrating changes produced in the blastula by increasing yolk mass. Fig. 13, *Ophiothrix*, a non-yolky type (after MacBride, 1907); Fig. 14, *Ophiura*, a moderately yolked type (after Grave, 1916); Fig. 15, Kirk's ophiuroid, a heavily yolked type (Fell, 1941).

In the moderately yolky type *Ophiura*, as described by Grave (1916), shows a thick-walled blastula with somewhat reduced blastocoel. The disposition of the nuclei shows that there is a tendency to form a blastula wall more than one cell deep— and in the later gastrula stage this tendency receives its full expression according to the earlier paper of Grave (1900) where he refers to the wall of the gastrula being more than one-cell deep. From the vegetal pole the mesenchyme in a reduced form bulges into the blastocoel, reducing its cross-section to a major segment of a circle.

Finally, in the heavily-yolked type we see in Kirk's ophiuroid the tendencies already weakly expressed in *Ophiura* reaching their fullest extent. The wall of the blastula is several cells thick. The blastocoel is reduced to a small cavity crescentic in vertical section owing to the bulging upward of the macromeres—obviously homologous with the mesenchyme producing cells of the other two forms.

The macromeres and micromeres occupy respectively the vegetal and animal poles as in the morula.

From this sequence we observe that with increasing yolk-mass the walls of the blastula become successively thicker, steadily reducing the blastocoel to a mere vestige in the animal hemisphere. The mesenchyme fails to separate as such but remains as a great bulging mass projecting upward into the blastocoel. As we see in the development that follows immediately upon this stage, the reduction of the blastocoel has a profound effect upon the process of gastrulation.

4. Formation of the Gastrula.

As the ontogenetic process advances the modifications produced in the larger and more yolky forms become ever greater. We thus find that the classical concept of evagination in the echinoderms becomes inadequate; for the evagination doctrine presupposes a static organogeny, whereas in actual fact organogeny is as dynamic and susceptible to moulding influences as any other biological process. Evolution, in other words, can act upon early stages of development as upon later stages. Embryological processes can be altered in the same way as can the adult products of these processes. This theory of the ability of evolution to act upon embryonic forms—so convincingly set out in de Beer's essay on " Embryology and Evolution " (1930)—receives strong support from the whole of the evidence provided by the yolky-egged ophiuroids.

Thus it is that in considering together the various types of gastrulation process met with in the Ophiuroidea we are able to detect the operation of a unidirectional evolutionary force, the strength of the force operating in direct proportion to the size of the yolk-mass. Whereas the doctrine of unchangeable recapitulation during development becomes meaningless in the light of such a process as is observable here, the view which envisages embryonic forms as essentially plastic and subject to a greater or less degree of modification—according to circumstance—provides, in the view of the writer, the only possible explanation of the facts observed.

The traditional concept of gastrulation in the echinodermata supposed that it takes place by invagination from one pole—the vegetal one. This is indeed true in the dwarf-egged group, such as *Ophiothrix* and *Echinus*. But, without any logical reason, it was then immediately assumed that such a process must also occur in all echinoderms.

The first voices raised against this rigid hypothesis were those of Apostolides (1882) and Russo (1891), who both claimed that the endoderm was formed by delamination in the embryo of *Amphipholis* (*Amphiura*) *squamata*. As it happens, their claim was based on a misinterpretation—as shown in the accompanying account of the development of that species—but the importance of their observation is that it demonstrated that gastrulation in *Amphipholis* certainly did not occur by means of simple invagination, for such a process when it occurs is unmistakable. However, their claim received no recognition, although it was never actually disproved. MacBride, in fact, dismisses the whole of Russo's account as " improbable in the highest degree," and omits it from his account of the echino-

derms in his " Text-book of Embryology " (1914). The very fact of such an attitude is itself a demonstration of the inadequacy of the Recapitulation Theory—which of course provided no explanation of the peculiar development of *Amphipholis*.

Grave (1900) gave reasons for believing that the endoderm in *Ophiura* arose not by the invagination of a hollow archenteron, but as a solid inpushing which later became hollowed out to form an archenteron. Certain stages were missing from Grave's material, however, and advantage was taken of this fact to throw doubts upon the accuracy of his work (Bather 1901, and MacBride 1907). In his later work, however, MacBride (1914) quotes Grave's account without comment. As is seen from the facts quoted below, Grave's account receives strong support from independent evidence derived from the study of Kirk's ophiuroid.

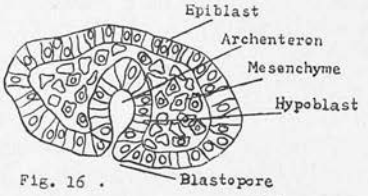


Fig. 16 .

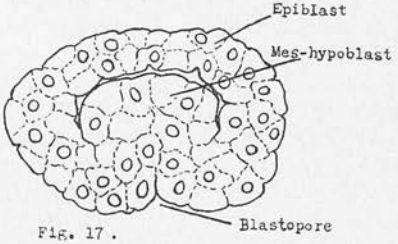


Fig. 17 .

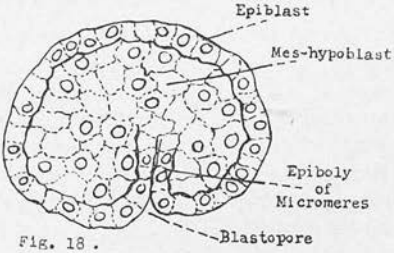


Fig. 18 .

FIGS 16–18.—Effect on gastrulation of increasing yolk mass. Fig. 16, gastrulation in *Ophiothrix* (after MacBride); Fig. 17, first stage in gastrulation of Kirk's ophiuroid. Fig. 18, second (*epibolic*) stage of gastrulation in Kirk's ophiuroid. Figs. 17 and 18 simplified from Fell (1941).

In the latter species gastrulation takes place by means of two processes. First, as shown in Fig. 17, there is a slight inpushing of the macromeres from the vegetal pole. This results in the complete obliteration of the small blastocoel. The macromeres which were pushed in remain a solid mass of cells without any cavity. So far the process is similar to that described by Grave in *Ophiura*. A second process commences now and involves extensive epiboly

of the micromeres, which migrate towards a central point on the vegetal hemisphere and then turn inwards (see Fig. 18). The point at which the inwandering of these micromeres takes place obviously is homologous with the blastopore, and a temporary small depression at that region is all that represents the archenteron. At a very much later stage a second cavity appears and extends as an excavation up through the solid endoderm mass to form the definitive enteron.

To sum up, the effect of increasing yolk-mass upon the process of gastrulation has been, first, to modify invagination till it takes the form of a solid inpushing of cells. At a later stage an excavation in this mass produces the definitive enteron. This modification applies both to the moderately yolky type (*Ophiura*) and to the heavily yolked type (Kirk's ophiuroid). In the case of the latter, however, the modification proceeds to a further stage, for the small blastocoel makes it mechanically impossible to invaginate all the endoderm, and hence a secondary process of epibolic inwandering of the micromeres takes place, surrounding and enclosing the whole of the vegetal hemisphere.

5. The Critical Point in Development.

We have now reached the critical point in the development at which the forms with direct development diverge from the forms with a larval stage or with a vestige of a larva. Whereas the former proceed to adopt radial symmetry immediately after the conclusion of gastrulation, the latter begin to assume bilateral symmetry, and retain it for a greater or less period till it is finally obliterated by radial symmetry. At first sight it would seem that there is a complete hiatus separating the two types of development—but in the view of the writer, this is illusory. An important question that this paper seeks to elucidate is how it is that direct development has been brought about. The point is discussed in the following section.

6. The Disappearance of the Larva from Ontogeny.

One of the proofs of the evolution theory cites the existence of " chains " or " series " of species showing, by small gradations, a progressive directional change. If the theory of receding metamorphosis outlined below be true, then we can reasonably expect to find some evidence of the existence of such a series of forms illustrating stages of the process. A survey of ophiuroid larval forms shows that such a chain does indeed exist.

We may take as the starting point of the bioseries a fully developed larval form such as the Ophiopluteus of *Ophiura albida*. Here there are four pairs of larval arms each supported by slender calcite skeletal rods (see Fig. 19a). The four pairs of arms are—the anterolateral, the postoral, the posterodorsal and the posterolateral. There is a mouth communicating by the stomodaeal oesophagus to the stomach, from which a short intestine leads to the anus. To the left lies the five-lobed hydrocoel.

A second term in the bioseries is illustrated by the larva of *Amphiura filiformis* (Fig. 19b), in which the posterodorsal arms have disappeared, and at the same time the postoral pair have become reduced in size. The other features remain unaltered.

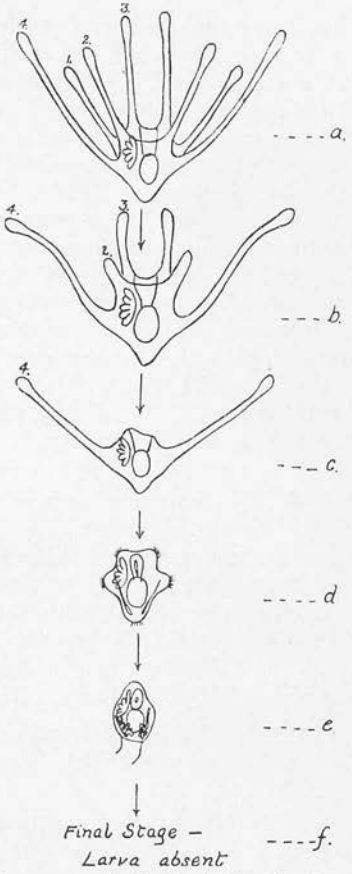


FIG. 19.—Sequence of Ophioplutei showing successive stages in the reduction and loss of the larva. a, first stage—e.g., *Ophiura albida;* b, second stage—e.g., *Amphiura filiformis;* c, third stage—e.g., *Ophiura affinis*; d, fourth stage—e.g., *Ophiopluteus claparèdei;* e, fifth stage, *Amphipholis squamata;* f, final stage, larva absent and development direct—e.g., Kirk's ophiuroid. The numbers above the larval arms indicate the order in which these organs disappear from the larva.

Next we may select the larva believed to belong to *Ophiura affinis* (Fig. 19c), in which the postoral arms have disappeared altogether, and the anterolateral pair also. Thus the last pair to disappear will be the posterolateral.

In the larva known as *Ophiopluteus claparedei* (the parent species being unknown) we have the stage in which the posterolaterals have indeed disappeared. That the posterolaterals should be the last to go is of particular interest, because in the metamorphosis of *Ophiothrix fragilis* it is this pair which is the last to be lost. This peculiar armless larva was taken by Claparede (1863) swimming on the surface of the sea off the coast of Normandy. In his description

of the animal he confuses the hydrocoel with a developing young ophiuroid, owing to its five lobes, but his accurate rendering of the organ in the figure makes clear its true nature. He records that there is a mouth opening, but apparently the anus has disappeared for he does not figure or mention it. At the aboral end are at either side two spicules, clearly vestiges of the skeletal rods of the arms. At the aboral apex, and on each of the two pairs of projecting " shoulders " are tufts of cilia. There can be no doubt that these shoulders represent the two main regions whence the arms arise in the fully developed species. But the most significant fact recorded in his account is the fact that the larva was so opaque (" undurchsichtig ") that the internal organs were somewhat obscured. Now this opacity undoubtedly indicates the presence of yolk in the tissues, and here we have the first indication of the point in the series at which increasing yolk began to be of importance. The reduction in the alimentary canal is complementary to the presence of yolk (Fig. 19d).

A further step in this sequence brings us to such forms as *Amphipholis squamata* where the reduction has proceeded so far as to obliterate all traces of arm roots and cilia, leaving only a vestigial pair of skeletal meshes, recognisable as vestiges of the arm rods by their position and inclination, but having lost the slender spicular form. The mouth opening has now disappeared, the alimentary canal being thus vestigial. The yolk mass has increased so as to make the larva quite opaque until artificially cleared (Fig. 19e).

The endpoint in the series is represented by such forms as Kirk's ophiuroid, in which the larval stage has disappeared entirely from development (Fig. 19f).

For this process of shifting backwards of the time at which radial form is assumed I suggest the term " Recession of Metamorphosis ".

A further indication that this has actually occurred is provided by the hydrocoel. As is well known, the time at which metamorphosis first commences is indicated by the behaviour of the hydrocoel. For this organ moves from its position on the left side of the gut and begins to encircle the oesophagus, its five lobes becoming the five radial canals of the adult. As recession of metamorphosis proceeds, the encirclement takes place relatively earlier in the life cycle, till in the directly developing form it appears right from the beginning as a canal encircling the future oesophagus (Fell, 1941).

This process of earlier and earlier metamorphosis is in reality a species of neoteny—the larva becoming " adult," as it were, at successively earlier and consequently undeveloped stages. A general diagram (Fig. 20) illustrates graphically the effect of recession of metamorphosis in ophiuroids.

It might be argued that the sequence of larval forms described above represents not a regression but a progression. This view would regard the fully developed *Ophiopluteus* as being a later evolutionary product derived from the simpler forms of larva, such as is found in

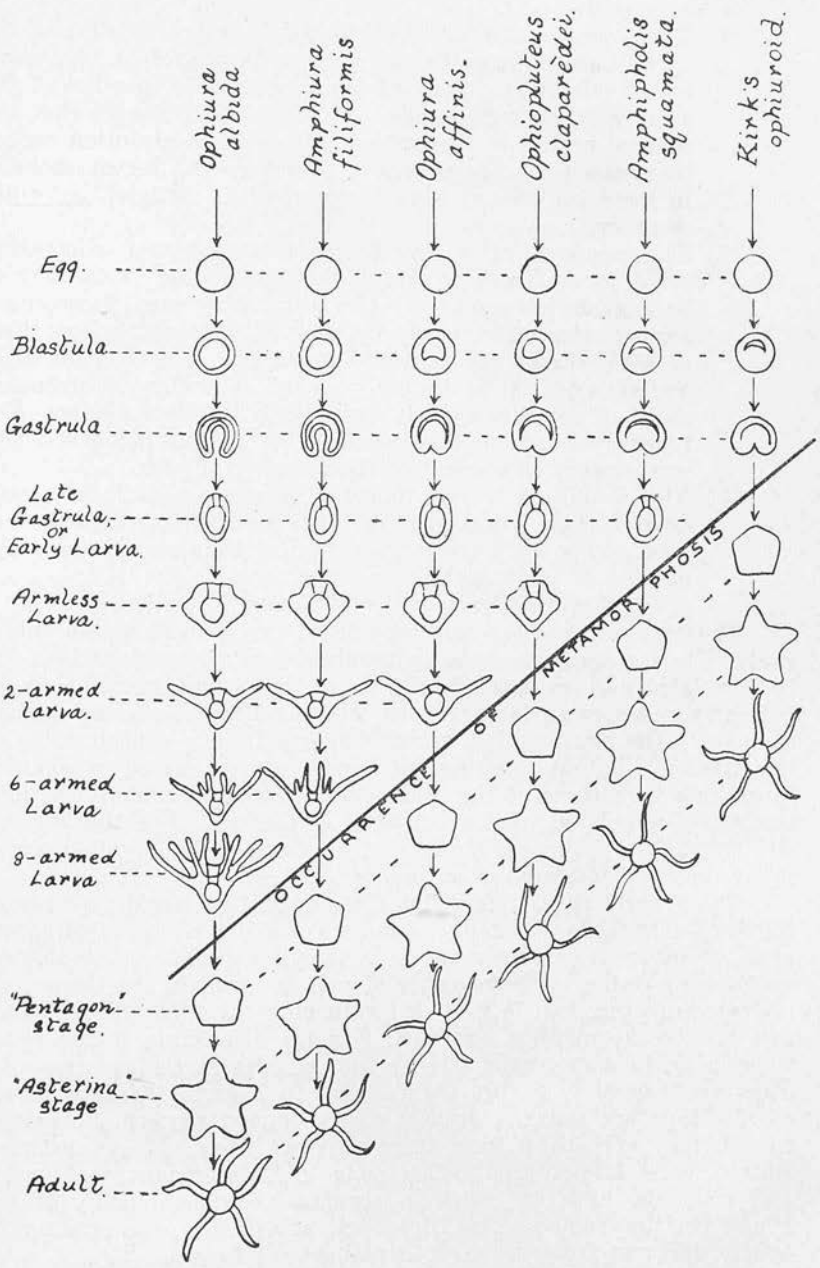


FIG. 20.—Diagram illustrating recession of metamorphosis into successively earlier stages, with resultant shortening of the development.

Amphipholis squamata. The following reasons seem to make such a view untenable:—

(1) The presence of what is obviously the representative of the larval arm-skeleton in the armless larvae of *A. squamata* and *Ophiopluteus claparedei* points strongly to a loss of the arms in these two species. It is very improbable that the skeletal organs of the arms would arise in evolution earlier than the arms themselves. Therefore the larval skeleton in these two species is to be regarded as vestigial, not rudimentary.

(2) The presence of a closed and non-functional alimentary canal in the larva of *Amphipholis squamata* is unlikely to be a primitive condition. An alimentary canal is required for digestion of food only by non-yolky larvae, such as those of *Ophiothrix fragilis* where it becomes necessary to swim and obtain food at an early stage. The closed alimentary canal of *A. squamata* is more likely to be a vestige of a formerly functional organ which has become physiologically unnecessary as a result of the presence of yolk.

(3) The simplified larvae, and the species which lack larvae, develop from yolky eggs of large size. It is unlikely that large yolky eggs are more primitive than small, non-yolky ones.

7. The Vitellaria or "Yolk-Larva" Series.

The bioseries we have just considered covers most of the ophiuroids. There remains, however, a peculiar divergent series which can be correlated with no larval series at all, but which nevertheless involves free-swimming larval forms with unmistakable characters in common. The amazing fact which emerges from a consideration of the literature is that this peculiar larval form is shared in common by no less than three of the echinoderm classes. Furthermore, it is invariably associated with a yolkmass in the egg. For this distinctive larval form I propose the term "Vitellaria"—or "yolk-larva"; it can only be considered as an independent sequence.

The general characters which distinguish this larval type are as follows:—The body is simply organised, having no pairs of larval arms, or other projecting organs. It is cylindrical or barrel-shaped, and opaque owing to the presence of yolk-material in the tissues. It is free-swimming, and is provided with rings of cilia. These bands are variable in number, but their general disposition is the same. There may be a larger or smaller tuft of cilia at the anterior end. They are commonly deeply pigmented. In Figs. 21–24 four larvae of this type are shown together; their common pattern is obvious, though they are drawn from three different classes of echinoderms. Indeed, these larvae, though belonging to Holothurians, Ophiuroids and Crinoids, have far more in common than have many of the Plutei or Bipinnariae. The Bipinnaria of *Asterias*, for example, is widely different from the great Bipinnaria of *Luidia*.

Hitherto in the literature these various forms have been considered separately. The Vitellaria is found among the Crinoids, and from that group no other larva is as yet known. Of Ophiuroidea, species of *Ophiura* are known to possess the larva in both America

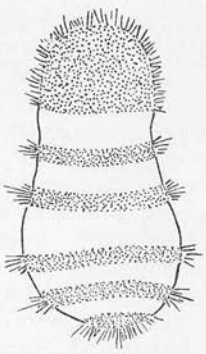


Fig. 21

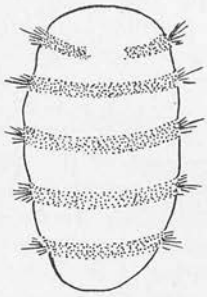


Fig. 22

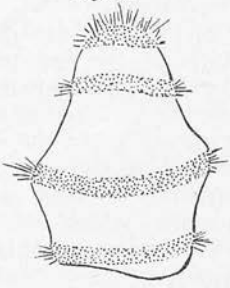


Fig. 23

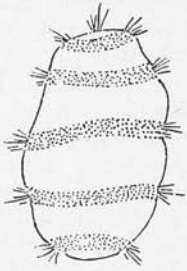


Fig. 24

FIGS. 21–24.—Examples of echinoderm "yolk-larvae." Figs. 21 and 22, of Holothuroidea (*Cucumaria* and *Labidoplax*); Fig. 23, of Ophiuroidea (*Ophiura brevispina*); Fig. 24, of Crinoidea (*Antedon bifida*). Fig. 21, after Selenka; Fig. 22, after Dawydoff; Fig. 23, after Grave; Fig. 24, after Seeliger.

and Europe. It is the same as "The Worm-like Larva" of Muller, a fact first pointed out by Grave. Among the Holothuroidea, some species possess only the Vitellaria ("Barrel-shaped larva" or "pupa"), while others possess an Auricularia which later becomes a Vitellaria.

In view of the diverse internal organogeny it is impossible to regard the Vitellaria as representing any ancestral type. It seems to be a generalised yolk form developed independently by the various classes under some special circumstances of which we have no information. The circumstances, whatever they may be, are undoubtedly connected with the yolk mass common to them all, but why the larva should assume such a typical annulated form in each case is a problem. It is evidently an example of convergent evolution affecting the larval forms without changing the adult—that is, without leaving its impress upon phylogeny. The process by which the Vitellaria is developed is therefore yet another example from the echinoderms of the mechanism termed by de Beer "Clandestine Evolution".

8. Ontogeny of the Coelom.

In parallel with the doctrine that gastrulation always takes place by invagination, there has grown a second doctrine equally

dogmatic that the coelom of echinoderms is always formed enterocoelously from pouches nipped off from the archenteron. Russo (1891) again was the first to state that the perivisceral coelom arose in *Amphipholis squamata* by a process of splitting in mesenchyme. It is instructive to note the way in which his results came to be ignored and forgotten. MacBride (1892) in his own paper on the very late stages of development of the same species makes no mention of the earlier development whatever. He does, however, mention that "... the coelom in *Amphiura squamata* is represented at first by a mass of mesenchyme; and as this condition of things is certainly not primitive, I do not think that even if reliable results as to the development of the cavities originating before the coelom clears were obtainable, they would be of much phylogenetic importance." The reasoning here is very confused. First, there is no proof that the mode of origin of the coelom in *Amphipholis* is not primitive—for, as shown in my analysis at the beginning of this paper, there are as many directly developing echinoderms known to science as ones with indirect development. Secondly, MacBride expresses his opinion that any reliable results as to the development of the cavities originating *before the coelom clears* (italics mine) would not be of much phylogenetic importance. Here is a complete reversal in his attitude, for the only cavities which originate in the embryo before the coelom "clears" are the vestigial enterocoelous pouches! If, then, MacBride considers these vestigial enterocoels of little phylogenetic importance, why does he also regard the schizocoelous coelom as "certainly not primitive"?

However, it is clear from MacBride's next paper (1907) that he once more reversed his position, for he now proceeds to quote Metschnikoff's account of the enterocoels in *Amphipholis*, and uses this account to disprove Russo's later one. Still no actual reinvestigation has taken place of the development of *Amphipholis* to confirm or disprove Russo's account.

Finally, in MacBride's "Text-book of Embryology" (1914) Russo's results are rejected as "improbable in the highest degree"—though still no reinvestigation of Russo's work had been done. Russo's conclusions in regard to the origin of the coelom in *Amphipholis squamata* remained forgotten till, in the couse of my work on Kirk's ophiuroid, I was amazed to find the coelom originating as a schizocoel in a mass of mesenchyme. Such a mode of origin was of course foreign to embryological theory as taught in the text-books. Eventually I was able to obtain photostats of Russo's paper from the British Museum, and then the full similarity between his account and the conditions independently observed by myself became evident. My paper on the development of *Amphipholis squamata* contains the results of a reinvestigation of his work, and confirmation of his description of the origin of the schizocoel in mesenchyme (Fell, 1945).

Having thus described the rather belated recognition of a schizocoel in ophiuroid development, we can now pass to a comparison of the modes of origin of the coelomic cavities in the various types of development (see Figs. 25–27).

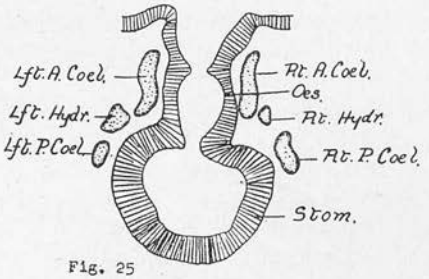


Fig. 25

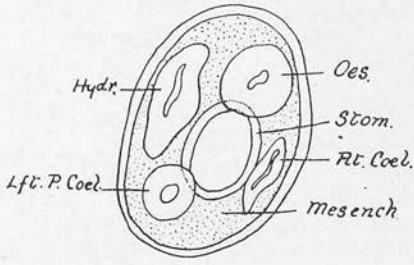


Fig. 26

FIGS. 25 and 26.—The enterocoels in *Ophiothrix* and vesicles of *Amphipholis*. In *Ophiothrix* (25) all parts of the coelom arise as enterocoelous vesicles. In *Amphipholis* (26) the number of vesicles is reduced, and none of them is an enterocoelous pouch. Only the hydrocoel survives, the other vesicles degenerating and contributing to the general mesenchyme, in which the remainder of the coelomic structures is later formed schizocoelously. Oes., oesophageal sac; Stom., stomach; Mesench., mesenchyme; Lft., Rt., Hydr., left and right hydrocoels; Lft., Rt., A. Coel., left and right anterior coelomic vesicles; Lft., Rt., P. Coel., left and right posterior coelomic vesicles.

In *Ophiothrix*, representing the non-yolky type, MacBride's description records that both right and left enterocoels form. The left divides into anterior and posterior parts, and soon afterwards the right does so also. From the posterior end of the left anterior coelom arises the hydrocoel. The wall of the left posterior coelom forms the arms, and its lumen the general coelom. The right coeloms become vestigial. MacBride also claimed that the right hydrocoel rudiments sometimes developed the five-lobe pattern, as does the left, but Narasimhamurti has since shown that this was a misinterpretation.

In *Amphipholis*, representing the moderately yolky type with vestigial larva, right and left enterocoels form. The right member disappears and the left gives rise only to the hydrocoel, and occasionally to a small posterior pouch which disappears later. The definitive general coelom arises by a process of splitting in an extensive mass of mesenchyme.

In Kirk's ophiuroid, where the embryo is heavily yolked and the larval stage completely omitted, both hydrocoel and general coelom

and its derivatives arise by splitting in mesenchyme. The hydrocoel is the first to form, and the embryo is free-living for some days before any general coelom commences to form.

In *Ophiomyxa brevirima* a closely similar condition holds, the coelom being preceded by an extensive zone of mesenchyme (Fell, 1940 b).

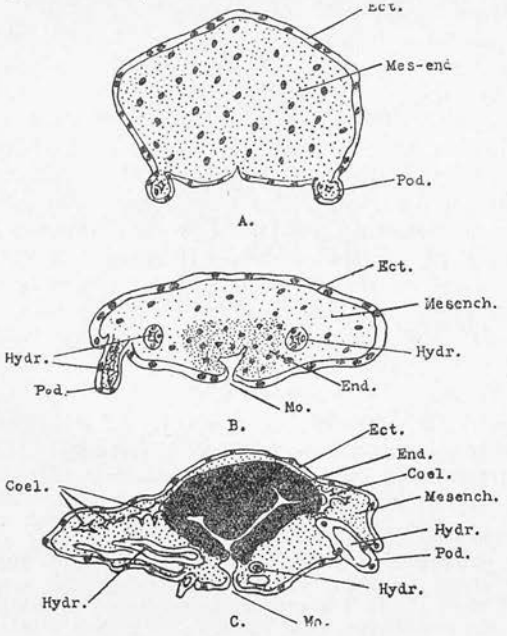


FIG. 27.—Schizocoelous origin of the coelom in a directly developing ophiuroid (Kirk's ophiuroid). A, the "rosette" stage, a solid gastrula assuming radial symmetry, and with budding podia; B, later stage, with the hydrocoel developing as a system of splits in the mesenchyme; C, general coelom developing by splitting in mesenchyme at a later stage than B. All represented in vertical section. Simplified from Fell (1941). Ect., ectoderm; Mes-end., mes-endoderm; Pod., podium; End., endoderm; Mo., mouth; Hydr., hydrocoel; Coel., general coelom; Mesench., mesenchyme.

To sum up, we note that as the yolk mass increases so does the tendency to form an enterocoel decrease. The hydrocoel lingers on longest as an enterocoel, but in the heavily yolked types it, too, arises by splitting, and is thus a schizocoel.

As noted in my paper on *Amphipholis*, the structures termed for convenience "enterocoels"—as they are clearly homologous with the enterocoels of *Ophiothrix*—are in fact formed by a splitting in small, solid masses of tissue formed on either side of the archenteron. Thus we have a series leading from the enteric pouches with preformed internal cavity, through enteric tissue-masses which later acquire an internal cavity, to finally the forms where the whole definitive coelom arises by an extensive process of splitting in a mesenchyme mass.

Whether it is the schizocoelous or enterocoelous method of coelom formation that is the more primitive is a matter of personal opinion. In the view of the writer it is the enterocoelous method which is secondary. My reasons for this were set out in a previous paper (Fell, 1940a), and need not be elaborated here.

9. Later stages in Development.

With the foundation of the coelom and its derivatives the principle phases of early development are completed. The later stages in development are fundamentally similar in all the types. In the yolky forms the yolk spherules gradually disappear from the peripheral tissues to become localised in the mesendoderm region, where they are finally absorbed. Skeletal formation is essentially the same in yolky and non-yolky forms.

10. Viviparity as a Factor Producing Direct Development.

It is clear that viviparity must act as a factor producing direct development for the simple reason that it automatically effaces the pelagic stage from the ontogeny. It had been my hope that my study of the development of *Amphipholis squamata* would provide material for understanding the effects of viviparity. Unfortunately, however, *Amphipholis*, as already noted, has a yolky egg, and practically all the alterations in development noted are attributable to this factor. The only other viviparous ophiuroid of whose development we have much information is *Ophiomyxa brevirima*, of which I hope to publish a further paper at a later date. Here again the embryo proves to be extremely yolky and has a schizocoelous coelom (Fell, 1941). Indeed, from such facts as we possess at present, it seems that a yolky egg is a condition frequently associated with viviparity in ophiuroids.

One result of viviparity, however, is certain. This is, that the young sea-star is enabled to pursue its development to a much more advanced stage in the viviparous forms, before emerging into the outer world and seeking its food itself. Thus, in *Amphipholis squamata*, the newly born star has arms with ten to fourteen arm-segments, whereas the newly metamorphosed star of oviparous forms is still in the unsegmented " Asterina " condition.

By means of experimental culture in vitro of explanted embryos of *Amphipholis squamata* it was shown that the embryo is unable to develop on its own yolk material alone (Fell, 1940 b). Certain substances must be added to the culture medium to enable normal development to proceed. This result taken in conjunction with anatomical evidence led to the conclusion that the developing embryos in *Amphipholis* are nourished by a secretion from the wall of the bursa. Here, then, is one undoubted effect of viviparity upon development in Ophiuroidea—that of prolonging embryonic life to a later stage by the secretion of nutritive substances. This effect is well illustrated by the following data:—*Ophiocomina nigra*, a non-yolky form with pelagic Ophiopluteus, has a functional alimentary canal by the third day, and continues to take in food for the remaining 35 days of larval life, before metamorphosis. A similar food-gathering larval period is found in *Ophiothrix fragilis*, which also has a func-

tional alimentary canal by the third day, and metamorphoses at about the twenty-sixth day. In the case of Kirk's ophiuroid, which is well provided with yolk, food is not taken in till the stage of about six arm-segments (i.e., when about twelve weeks old). In *Amphipholis squamata*, where the viviparous condition is found, the young ophiuroid does not seek food for itself till it has reached the stage of having about twelve arm-segments (i.e., when probably about six months old, on the supposition that it develops at a similar rate to other ophiuroids).

Beyond this conclusion there is insufficient evidence available as yet of the effect upon development in echinoderms of viviparity. Whatever its influence, the effect of increasing yolk-mass has apparently brought about the major portion of the modifications in development.

11. The Mechanism Which Has Brought About Direct Movement.

In the foregoing analysis of the developmental phases of ophiuroids it has been shown that the principle agent tending to produce direct development has been an increasing yolk-mass. One striking fact is the uniformity of the changes produced in diverse groups of ophiuroids—ranging from one of the most primitive species such as *Ophiomyxa brevirima* to the more specialised types. The modification of the gastrulation process, the suppression of the larva, and the increase in mesenchyme in which a schizocoel comes to form are some of the salient features of the yolky-egged forms.

The truly remarkable parallels which are observable in the embryonic stages of these various unrelated ophiuroids which have been influenced by accumulating yolk suggest very strongly that there exists some common principle which has operated in a common way upon these diverse forms. Before suggesting a possible answer to the problem of what this principle may be, it will be convenient to summarise the main stages in the sequence of forms showing reduction and loss of the larval stage.

We see in this sequence a progressive reduction in the size and number of the larval arms followed by reduction and final loss of the arm skeleton. Then comes reduction of the coelomic pouches on either side, with a corresponding increase in the mesenchyme mass in which the coelom alternatively develops by splitting. Finally there is complete loss of bilateral symmetry, loss of the larval stage, loss of the vestigial enterocoels, and both general coelom and hydrocoel develop by splitting in the mesenchyme mass, which becomes increasingly important.

Now, in this progressive retreat inwards of the bilaterally disposed elements of the larval body with simultaneous recession of the radial symmetry into the earlier stages, we have a process suggesting alterations in the axial gradients of the embryo, these alterations being progressive along the series. Considering the modifications of development in this light, the following explanation may be put forward to explain the nature of the mechanism involved.

If we suppose that in the course of the evolutionary history of these larval forms changes began to take place in the metabolism along the axial gradients on either side of the body of the larva,

the changes being in the nature of inhibitions, then a reduction and final loss of the organs on either side would occur—larval arms, skeletal rods, coelomic pouches; in other words, the bilateral symmetry would become gradually submerged, and the point at which radial symmetry was assumed would undergo a recession towards the gastrula stage. This is precisely the sequence of events which, it has already been suggested, has actually occurred. Thus, an inhibitory influence acting upon the earlier stages of development is sufficient to bring about entire loss of the larval stage.

Here, as in all theories, a useful test is the inductive one. What evidence have we that such a process can take place? Is there experimental evidence? The answer is, I believe, supplied already by the work of Child (1916). In the course of experimental work upon the plutei and earlier embryos of echinoids this worker was able to show that a wide range of simple chemical substances could cause an inhibitory effect very similar to that which has been postulated above. He was able to produce sea-urchin plutei showing successive degrees of reduction and obliteration of antero-posterior, medio-lateral and apico-posterior differences through inhibitions of the axial metabolic gradients. In extreme cases his larvae resembled somewhat the peculiar armless larvae already referred to in this paper. Child drew from his work the deduction that the larval forms of echinoderms may have been evolved by increases in the metabolism along the metabolic gradients, producing the outgrowths of the arms, etc. Combining his results with the sequence of forms described in this paper, we can similarly add that the larval forms of echinoderms may have been secondarily lost again through inhibitions in the same axial gradients. The inhibitory substance may have been developed in close association with the production of the yolk material, or it may be that the yolk material itself provided the inhibitory influence.

A further parallel remains. Child found that the inhibitory effects were differential—acting to a variable degree on various tissues. Mesenchyme he found was comparatively unaffected, and consequently underwent a great increase in his larvae at the expense of the bilateral organs which became reduced. Now this is also closely similar to the effect noted in the transition from indirect development to the direct type. With reduction and disappearance of the larva there has been a corresponding increase in the amount and importance of the mesenchyme.

Therefore, in the view of the writer, there is good reason to believe that direct development in echinoderms has been produced by an inhibitory influence upon the axial metabolic gradients of the larva. The inhibitory influence is associated with an increasing yolk-mass, and has manifested itself through a steady recession of the metamorphosis towards the gastrula stage.

SUMMARY.

1. Direct development in the Echinoderma is no less typical than development of the indirect, larval type. Of the five living classes of echinoderms, only the Echinoidea are characterised by being predominantly of the indirectly developing type.

2. Increase in volume of the ovum is directly related to increase of the cytoplasm and its product, the yolk-mass. With increasing egg-size and amount of yolk, there has arisen a steadily increasing tendency to have direct development.

3. The increase of yolk has not greatly modified the process of cleavage, as segmentation in all forms is total. There is, however, a tendency to form micromeres and macromeres with increasing yolk-mass.

4. With increasing yolk-mass the wall of the blastula becomes steadily thicker and the blastocoel becomes reduced to a vestige in the animal hemisphere. The mesenchyme fails to separate as such but projects in a solid mass into the blastocoel.

5. The effect on gastrulation of increasing yolk-mass has been, first, to reduce invagination to a solid inpushing of cells; and, secondly, to bring about a subsequent epibolic inwandering of micromeres to contribute to the mesendoderm. The archenteron becomes vestigial and the definitive enteron is later excavated in the solid endoderm by a process of splitting.

6. A succession of stages in the reduction of the Ophiopluteus makes it probable that by a recession of the metamorphosis towards the gastrula stage, the larval period has been shortened, and finally lost altogether.

7. The recession of metamorphosis has resulted in the extreme case in radial symmetry being adopted immediately after the completion of gastrulation. This occurs in Kirk's ophiuroid.

8. A collateral and independent evolution has been followed by certain echinoderms with yolky eggs, resulting in the formation by convergent evolution, of a special yolk-larva, termed in this paper the "Vitellaria". This process has taken place in the Holothuroidea, Crinoidea and Ophiuroidea, independently in each case. The Vitellaria is characterised by its cylindrical form, opacity due to yolk material present in the tissues, the complete absence of larval appendages, and the development of transverse rings of cilia.

9. With increasing yolk-mass there has occurred a reduction and loss of the enterocoels, with a corresponding increase in the amount of the mesenchyme: in this latter tissue the coelomic cavities arise by schizocoelous intercellular splitting. The hydrocoel is the last enterocoel to remain as such.

10. Viviparity appears to have been only a secondary factor in producing direct development. It has chiefly acted through prolonging embryonic development by enabling the embryo to obtain nourishment from the parent.

11. The suggestion is made that the mechanism of direct development has been an inhibitory influence upon the axial metabolic gradients of the larva. The inhibitory influence must be closely related to the presence of a yolk-mass and it has manifested itself through a steady recession of the metamorphosis toward the gastrula stage.

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ECHINODERM EMBRYOLOGY AND THE ORIGIN OF CHORDATES

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In this article it is proposed to review some recent researches in echinoderm embryology, with special reference to their bearing on the evolution, specialization and omission of larval forms, together with an appraisal of the embryological evidence for the supposed echinoderm origin of chordates.

I. THE PLASTICITY OF THE LARVAL STAGE

1. *Larval morphology*

The fundamental features of the development and interrelationships of echinoderm larvae, as worked out during the latter part of the nineteenth century, were derived from the initial brilliant researches of Johannes Mueller (1846 *et seq.*) who demonstrated that the four main types arise in each case from a simple *dipleurula* form. Ignoring at present the coelom, which is discussed later, the basic plan of development is represented in Fig. 1. The dipleurula arises from a preceding gastrula stage by the formation of a ciliated (or vibratile) band (Fig. 1 A) which forms a closed loop about the mouth. A simple alimentary canal is present, comprising stomodaeum, archenteron or stomach, and proctodaeum; the anus is generally, but not always, formed from the blastopore. In its subsequent development the dipleurula undergoes a varying transformation according to the systematic position of the parent species.

In the classes Echinoidea and Ophiuroidea the development of paired arms or processes on either side of the body, upon which the ciliated band becomes extended, leads to the formation of the *simple pluteus* (Fig. 1 B). Further development of paired arms, strengthened by internal calcareous rods, leads to the final larval forms, distinguished by Mortensen (1898) as *echinopluteus* and *ophiopluteus* according to the class.

The echinopluteus usually possesses four pairs of arms (Fig. 1 C), though more or fewer may be present in certain forms. The four principal pairs of arms comprise

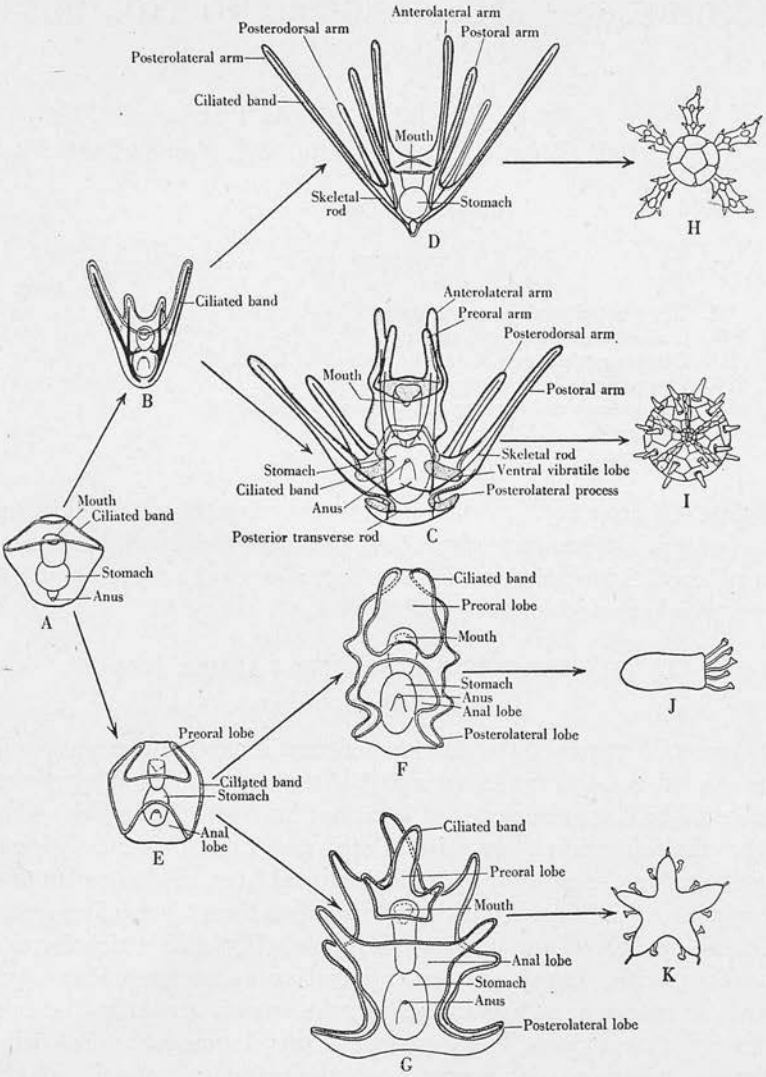

Fig. 1. General scheme indicating the relationships of bilaterally symmetrical echinoderm larvae. A, dipleurula. B, pluteus. C, echinopluteus, which metamorphoses into a young echinoid, I. D, ophiopluteus, which metamorphoses into a young ophiuroid, H. E, early auricularia. F, fully developed auricularia, which metamorphoses into a young holothurian, J. G, bipinnaria, which metamorphoses into a young asteroid, K.

two anterior pairs, the anterolateral and preoral pairs, and two posterior pairs, the postoral and posterodorsal pairs. In addition, at the extreme posterior end of the body are commonly found a pair of posterolateral processes, which are occasionally

elongated to form distinct posterolateral arms. Anterodorsal arms occur in certain cases as a still further complexity (compare Fig. 5 I, a spatangoid echinopluteus). These various arms are supported by slender calcareous rods, which may form a mesh about the archenteron at their inner extremities within the body; often a special posterior transverse rod is formed between the posterolateral processes. Certain portions of the ciliated band may become thickened dorsally and ventrally to form the paired dorsal and ventral vibratile lobes; or these may become separated from the main band to form prominent epaulets, as in Fig. 5 G.

The ophiopluteus (Fig. 1 D), if fully developed, is of rather similar appearance, having four pairs of arms, which however do not correspond altogether with the four pairs commonly present in the echinopluteus. It is usually the case that the most prominent and enduring arms are those which are termed the posterolateral pair, which Mortensen has shown to be homologous with the posterolateral lobes of the echinopluteus as normally formed. The other arms are the anterolateral, the postoral and posterodorsal pairs respectively. The preoral arms of the echinopluteus are not represented. The internal skeleton takes the form of a pair of calcareous rods in the body, each sending branches into the four arms on its corresponding side; the posterior transverse rod is not represented.

In the classes Holothuroidea and Asteroidea no comparable development of paired arms occurs. Initially the dipleurula becomes rather barrel-shaped (Fig. 1 E), and the ciliated band is thrown into folds in an anterior and posterior loop. Further sinuous growth of the ciliated band leads to the characteristic larval forms, the *auricularia* in holothurians, and the *bipinnaria* in asteroids.

The auricularia (Fig. 1 F) is characterized by the formation of two lobes bordered by the folded ciliated band, the preoral lobe anteriorly, and the anal lobe posteriorly, the latter bearing the anus. The mouth lies in a depression on the ventral side, between the preoral and anal lobes. Smaller posterolateral lobes occur in the same relative position as in the preceding larvae.

The bipinnaria is much more variable in structure. Sometimes, especially in primitive starfish, it is scarcely distinguishable from the simple auricularia. More frequently the sinuous lobes of the ciliated band become drawn out into prominent arms (Fig. 1 G) which, however, lack skeletal rods. Consequently they are not rigid, and are utilized as flexible swimming organs. Posterolateral lobes are usually found as in the auricularia. Median arms often appear anteriorly to the mouth, on the preoral lobe. It is usual for the bipinnaria stage to be followed by what is termed a *brachiolaria* larva, distinguished principally by the development of median sucking arms (or disk), anterior to the mouth, by means of which the larva may become temporarily attached.

In each case metamorphosis involves either discarding or absorbing the paired larval structures, while a secondary radial symmetry is initiated through encirclement of the gut by the five lobes of the hydrocoel.

The embryology of crinoids, so far as is known, does not include a comparable bilaterally symmetrical larva, and the mode of development is so different that it

cannot be treated in the scheme above. As will be further noted later on, a large proportion of echinoderms other than crinoids also undergo developments of an entirely different character from the basic plan outlined above. A frequent condition in forms with large yolky eggs is that the larva is a simple cylindrical form with a number of transverse ciliated bands. This type, which is sluggish and does not take food, has been termed the *vitellaria*. It is formed variously, and the internal organogeny differs according to the class.

Echinoderm larvae occasionally grow to a considerable size. Thus the bipinnaria of *Luidia sarsi*, i.e. the *Bipinnaria asterigera* of Sars (1835), reaches a length of 2·4 cm. A New Zealand form, *Auricularia nudibranchiata* of unknown parentage, measures at least 1 cm. in length (MacBride, 1920).

The above facts offer interesting problems. The general occurrence of a pelagic bilaterally symmetrical dipleurula stage in four of the existing classes has been interpreted as a recapitulation of a hypothetical dipleurula form, from which all echinoderms are supposed to have descended. This view has not been seriously questioned and remains acceptable to taxonomists and embryologists alike. But beyond this point matters are less clear. Are the succeeding larval stages to be interpreted in the same light? If so, we would be led to the conclusion that ophiuroids and echinoids, with their similar pluteus stages, are more closely related to each other than to any of the remaining classes. Neither taxonomic nor palaeontological evidence supports such a deduction. There can be little doubt that the ophiuroids are related to the asteroids through more generalized Palaeozoic stelleroids. The alternative is to regard the characteristic post-dipleurula larval stages as 'digressions' from the original path of development, which have arisen independently in the various classes by clandestine evolution—to use de Beer's term (1930) for evolution which does not affect adult forms. Mortensen (1921) regards these larvae as highly specialized adaptations of the original pelagic ancestral form, having been modified along with the adults, so as to form groups corresponding with the natural groups of the adults. I have suggested (Fell, 1945) that they have arisen in response to the need for a temporary food-gathering stage as a preliminary to further development; for they almost invariably arise from eggs which are deficient in yolk and cytoplasm. A more specific examination of modes of echinoderm development also leads inevitably to the conclusion that special larval evolution has occurred, often quite independently of natural groupings, as the following cases illustrate.

2. *Larval convergence*

It is instructive to compare the larval development of an ophiuroid such as *Ophiothrix*, well known through the work of MacBride (1907), with that of echinoids of the genus *Centrechinus* (*Diadema*) described by Mortensen (1931). The echinopluteus of the latter is greatly modified through unusual development of the postoral arms and reduction of the other arms, so that it superficially resembles an ophiopluteus (Fig. 2). This case, where adults so conspicuously distinct, and only remotely related, possess such surprisingly similar larval forms, permits of only one

interpretation: convergent embryonic evolution has occurred in the echinoid, which temporarily resembles an ophiuroid stage.

Even more striking is the case of the vitellaria larva (Fig. 3). This characteristic cylindrical larva with ciliated annulations, derived from a yolky egg, occurs in three

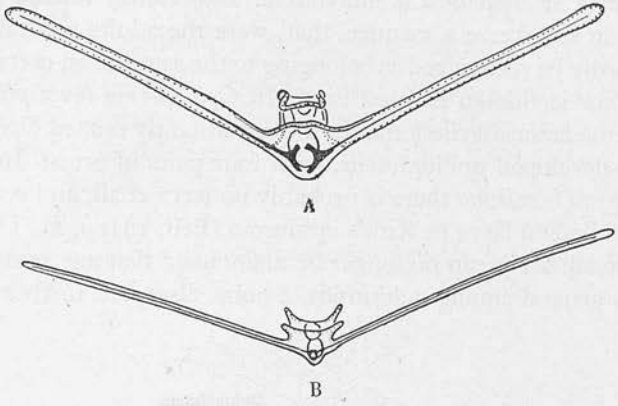

Fig. 2. Convergent larval forms. A, an echinoid, *Centrechinus* (*Diadema*). B, an ophiuroid, *Ophiothrix*.

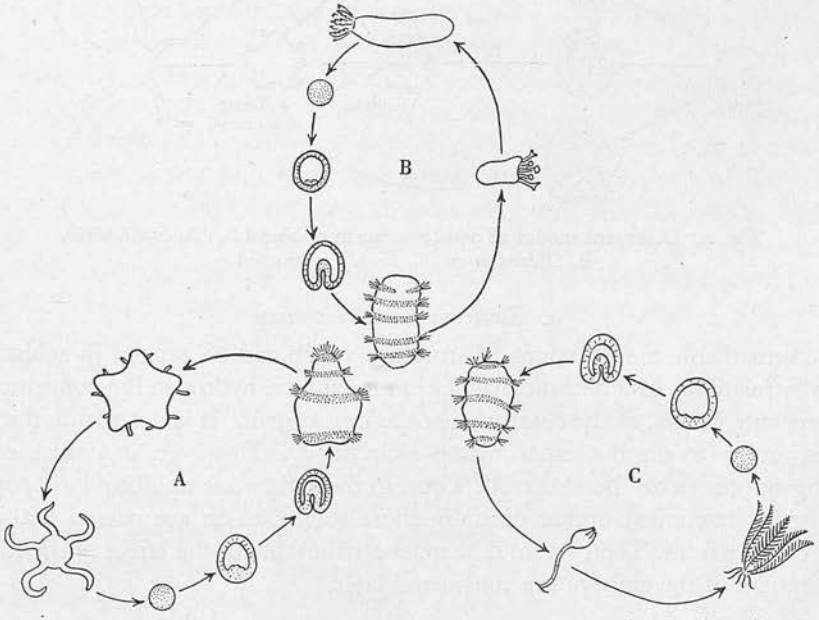

Fig. 3. Convergent development of unrelated echinoderms. A, class Ophiuroidea (*Ophioderma*). B, class Holothuroidea (*Cucumaria*). C, class Crinoidea (*Antedon*). In each case the larva is a vitellaria.

classes, the holothurians and crinoids commonly, and the ophiuroids rarely. Although Grave in 1903 regarded this larva as representing an original primitive form, such a view cannot be regarded as probable, for many obvious reasons.

3. *Larval divergence*

Divergent evolution in larval development is strikingly illustrated throughout the phylum. In ophiuroids, for example, quite diverse modes of development occur (Fig. 4). The case of *Amphiura* is illustrative. Two closely related species in this genus develop in so diverse a manner, that, were the adults unknown, the young stages could hardly be recognized as belonging to the same class, certainly not to the same genus. Nor is this an isolated case. In *Ophioderma brevispina*, studied by Grave in 1900, the larva is a vitellaria. In the not distantly related *Ophiura texturata* there is a well-developed ophiopluteus, with four pairs of arms. In other species such as *Ophiomyxa brevirima* there is probably no larva at all, and certainly there is no vestige of a bilateral larva in Kirk's ophiuroid (Fell, 1941 *a*, *b*). These variations are not exceptional, for it can no longer be maintained that any particular mode of development is general among ophiuroids, a point discussed further below.

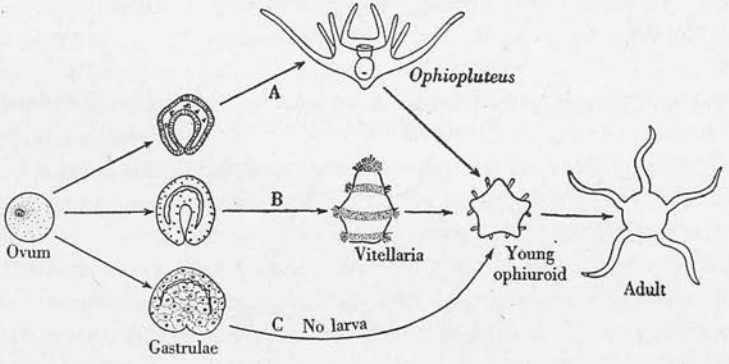

Fig. 4. Divergent modes of development in ophiuroids. A, *Ophiothrix*. B, *Ophioderma*. C, Kirk's ophiuroid.

4. *Environmental responses*

The remarkable modifications of structure which can be evoked in echinoderm larvae by relatively insignificant changes in the salinity, hydrogen ion concentration, oxygen content, etc., of the environment are well known. It is not within the scope of this review to discuss experimental embryology. However, in nature equally striking responses can be observed. Thus, in the viviparous ophiuroid *Amphipholis* embryonic attachment organs occur in those stages which are passed within the bursa of the parent. The profound changes attributable to the effect of the internal environment of the embryo are considered later.

5. *Conclusions*

Embryos and larvae of echinoderms are essentially plastic and susceptible to evolutionary modifications of structure which may act independently of the adult stage. For this reason phylogenetic deductions should not be based on larval forms alone.

Before considering possible causes for such modifications it is necessary to review some remarkable recent researches which have demonstrated how embryological evolution has occurred independently yet in parallel with adult evolution.

II. ECHINODERM LARVAE AND TAXONOMY

Researches leading to the conclusion that definite relationships can exist between the structure of adult echinoderms and that of their larvae have been carried out by Mortensen (1921 and later references). Thus in the Echinoidea the extant orders, and frequently families, can be characterized by the nature of the echinopluteus. To a lesser extent a similar relation is seen in Asteroidea. The position in the other classes is not so clear. These results, in conjunction with other relevant studies, are summarized in the following survey.

1. *Class ECHINOIDEA*

Order CIDAROIDEA

Until 1937 the development of cidaroids was known only very incompletely, and no general conclusions could be drawn as to its nature. The following species had been studied: *Cidaris cidaris* (Prouho, 1888), *Eucidaris tribuloides* (Tennant, 1922) and *E. thouarsii* (Mortensen, 1921). In addition, Mortensen (1921) had shown that the development of *Phyllacanthus parvispinus* is probably direct. In 1937 Mortensen published his account of *Eucidaris metularia*, and the following year that of *Prionocidaris baculosa*, which was studied through metamorphosis. The two latter accounts are the most important, and together with the earlier data enabled the conclusion to be drawn that there is a distinctive cidaroid larval form (Fig. 5 B). This is an echinopluteus characterized by the very long, smooth fenestrated postoral and posterodorsal rods; by having the posterior transverse rod provided with long, slender median processes dorsally and ventrally; and by the strong development of the ciliated lobes. A larval muscular system is present in the two latter species, enabling the two pairs of long arms to be moved backwards and forwards, and no doubt this feature is also generally characteristic of the cidaroid larva.

A further feature of morphological interest is that in the newly metamorphosed urchin of *Prionocidaris* a pluriserial interambulacrum occurs, as in Palaeozoic echinoids. These are later resorbed, as in *Archaeocidaris*, thus lending support to Mortensen's contention that *Archaeocidaris* and not *Bothriocidaris* is to be regarded as ancestral to the Cidaroidea.

Order CENTRECHINOIDEA (DIADEMOIDEA)

In this group of echinoids distinctive echinoplutei can be correlated with the families Centrechinidae (Diadematidae) and Arbaciidae. The development of the Echinothuridae and Salenidae remains unknown.

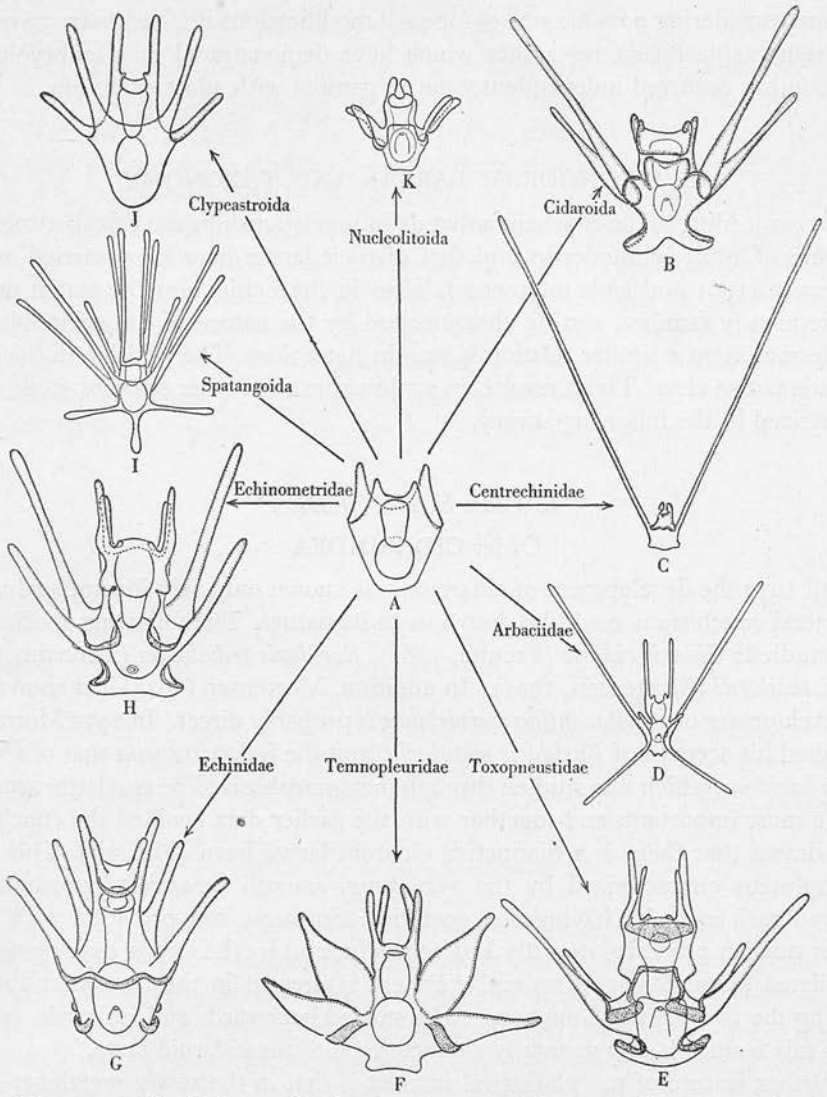

Fig. 5. Divergent echinoid larvae showing larval evolution corresponding to natural taxonomic groups based on adult forms. All are echinoplutei derived from the basal early pluteus form. For further details see text.

Family CENTRECHINIDAE

Knowledge of the development of these is due mainly to Mortensen. The following species have been investigated: *Centrechinus* (*Diadema*) *setosum* (Mortensen, 1931, and Onoda, 1936), *C. antillarum*, *C. savignyi* and *Echinothrix diadema* (Mortensen, 1931). It is now evident that the larva of these (Fig. 5 C) is of the form earlier characterized under the name *Echinopluteus transversus* (Mortensen, 1921) the parental species being at that time unknown. It is notable for the great development

of the postoral arms, the other arms being absent save for small anterolaterals which may be present. The larva thus strongly resembles an ophiopluteus. The ciliated band is not strongly developed, in sympathy with the reduction of the arms, and there are no vibratile lobes or epaulets. There are also other skeletal peculiarities which need not be specified here.

Family Arbaciidae

The development of three species of the genus *Arbacia* has been studied: *A. lixula* (J. Mueller, 1853; *et al.*); *A. punctulata* (Fewkes, 1880; Brooks, 1882; Garman & Colton, 1882); *A. stellata* (Mortensen, 1921). The arbaciid larva (Fig. 5 D) has at first a basket skeleton. In its second stage of development a posterior transverse rod is present ending in a pair of long posterolateral arms which are similar to the other arms. Postoral and posterodorsal rods are fenestrated. There are large ventral and dorsal lobes, but no epaulets.

Order CAMARODONTA

Distinctive echinoplutei are known for each of the families Temnopleuridae, Echinidae, Toxopneustidae and Echinometridae (using these in the sense proposed by Mortensen (1921), who regards *Toxopneustes* and its allies as constituting a distinct family, restricting the other families accordingly).

Family Toxopneustidae

Knowledge of the development of these is derived from studies of the following species: *Lytechinus variegatus* (Tennant, 1910; Mortensen, 1921); *L. anamesus*, *L. pictus*, *L. panamensis* (Mortensen, 1921); *L. verruculatus* (Mortensen, 1921, 1931); *Nudechinus gravieri* (Mortensen, 1937); *Toxopneustes pileolus* (Mortensen, 1921; Onoda, 1936); *T. roseus* (Mortensen, 1921); *Tripneustes esculentus* (Tennant, 1910; Mortensen, 1921); *T. gratilla* (Mortensen, 1921, 1931, 1937; Onoda, 1936); *Sphaerechinus granularis* (J. Mueller, 1855, *et al.*); *Pseudocentrotus depressus* (Mortensen, 1921; Onoda, 1936). Further, if *Strongylocentrotus* be admitted to this family, as Mortensen has suggested, the following four species may be added: *S. droebachiensis* (A. Agassiz, 1864); *S. franciscanus* (Loeb, 1908; Hagedoorn, 1909; Mortensen, 1921; Johnson, 1930); *S. purpuratus* (Hagedoorn, 1909); *S. pulcherrimus* (Mortensen, 1921; Onoda, 1936).

The echinopluteus of this assemblage possesses in its first stage a short body, usually with a basket structure of the skeleton. In its second stage (Fig. 5 E) there is a posterior transverse rod. Posterolateral arms occur, and also vibratile lobes, and epaulets at the bases of the four main arms. The rods of the main arms may be either simple or fenestrated (Mortensen, 1921).

Family Temnopleuridae

The following species have been studied: *Temnopleurus toreumaticus* (Mortensen, 1921; Onoda, 1936); *T. hardwickii* (Moore, 1933); *Temnotrema sculpta* (Mortensen,

1921); *T. scillae* (Mortensen, 1937); *Mespilia globulus* (Mortensen, 1921; Onoda, 1936); *Salmacis bicolor* (Aiyar, 1935).

In the first stage there is no basket structure of the skeleton. In the second stage (Fig. 5F) a posterior transverse rod forms, from which short branched posterolateral rods may or may not issue. There are four vibratile epaulets, but no vibratile lobes. The arms are often highly characteristic owing to a bloated condition (Mortensen, 1921).

Family ECHINIDAE

The development of several species of this family has been well known for a long time, although it was not till 1921 that Mortensen first defined the type of echinopluteus characteristic of the family. The following species have been studied: *Paracentrotus lividus* (J. Mueller, 1852; Metschnikoff, 1869 *et al.*); *Psammechinus miliaris* (MacBride, 1898; Mortensen, 1898; Theel, 1902 *et al.*); *P. microtuberculatus* (J. Mueller, 1852; Selenka, 1879; Giesbrecht, 1913); *Echinus esculentus* (MacBride, 1898, 1903; Shearer, de Morgan & Fuchs, 1914); *Parechinus angulosus* (Mortensen, 1931); *Echinus acutus* (Shearer, de Morgan & Fuchs, 1914); *Sterechinus agassizi* (Mortensen, 1913).

In its first stage the larva has a short body, usually with a basket structure of the skeleton. In the second stage (Fig. 5G) there is a posterior transverse rod; posterolateral and vibratile lobes occur, and also epaulets at the bases of the four main arms; the rods of the main arms may be either simple or fenestrated.

Family ECHINOMETRIDAE

The larval development of this family remained unknown until 1921, when Mortensen published accounts of nine species. Onoda (1931, 1936) has since added information on two other species. The following have been studied: *Echinometra lucunter* (Mortensen, 1921); *E. oblonga* (Mortensen, 1921); *Colobocentrotus astratus* (Mortensen, 1921); *Echinometra mathaei* (Mortensen, 1921, 1937; Onoda, 1936); *Heterocentrotus mammillatus* (Mortensen, 1921, 1937); *Heliocidaris tuberculata* (Mortensen, 1921); *H. crassispina* (Onoda, 1931); *Evechinus chloroticus* (Mortensen, 1921); *Stomopneustes variolaris* (Mortensen, 1931); *Echinostrephus molaris* (Onoda, 1936). To these may be added *Heliocidaris erythrogramma* for which Mortensen (1921) has given a partial account indicating that a form of direct development occurs.

The echinometrid larva has in the first stage the body short and obliquely truncate, supported by a complex basket structure. In its second stage (Fig. 5H) there is a posterior transverse rod present. Posterolateral and vibratile lobes occur, but no epaulets. The rods of the main arms are fenestrated (Mortensen, 1921).

Order NUCLEOLITOIDA

There are only two surviving species of this Mesozoic and early Tertiary group; of these *Apatopygus* (*Echinobrissus*) *recens* is found in New Zealand and Mortensen (1921) has given an account of the larval development, which

appears to indicate affinity with the clypeastroids. The fully developed larva is as yet unknown, but Mortensen's oldest stage is illustrated in Fig. 5 K.

Order CLYPEASTROIDEA

A series of fifteen species is available for comparison of their larval development, which has been shown to be of a characteristic type (Mortensen, 1921). The species are: *Echinocyamus pusillus* (Theel, 1892; Mortensen, 1931); *Fibularia craniolaris* (Mortensen, 1937); *Echinarachnius parma* (A. Agassiz, 1864; Fewkes, 1886); *E. excentricus* (Mortensen, 1921); *Peronella leseuri* (Mortensen, 1914; Tennant, 1915; Mortensen, 1921); *Clypeaster japonicus* (Mortensen, 1921); *C. humilis* (Mortensen, 1937); *Arachnoides zelandiae* (Mortensen, 1921); *A. placenta* (Feliciano, 1933); *Encope micropora* (Mortensen, 1921); *Mellita sexiesperforata* (Mortensen, 1921); *Astriclypeus manni* (Mortensen, 1921); *Laganum diplopora* (Mortensen, 1921); *L. depressum* (Mortensen, 1938); *Echinodiscus auritus* (Mortensen, 1937, 1938).

In the clypeastroid larva the body skeleton forms a prominent basket structure of distinctive character. This often takes the form of a large, complex, fenestrated plate in the posterior end of the body (Fig. 5 J).

Order SPATANGOIDEA

As is well known, the spatangoids are characterized by possessing a highly distinctive echinopluteus which bears a median unpaired arm-like process (Fig. 5 I). In addition, the anterodorsal arms are well developed. Mortensen (1921) has further suggested that it may ultimately be found that the two families Spatangidae and Brissidae have distinctive larvae, as from the data available it appears that the former possess posterolateral arms, while the latter lack these structures.

The following spatangoid larvae are known: Spatangidae—*Spatangus purpureus* (Krohn, 1853; Mortensen, 1913); *Echinocardium cordatum* (Mortensen, 1898, 1931; MacBride, 1913); *E. australe* (Mortensen, 1921); *Moira atropos* (Grave, 1902; Tennant, 1910); *Lovenia elongata* (Mortensen, 1937). Brissidae—*Brissus obesus*, *B. agassizi*, *Brissopsis lyrifera* (Mortensen, 1921); and, doubtfully identified, *Meoma grandis* (Mortensen, 1921).

2. *Phylogenetic implications of echinoid development*

The conclusions drawn from the above data by Mortensen may be quoted as given substantially in his main study (1921):

The Echinopluteus affords the greatest diversity of forms of all Echinoderm larvae, and several well-marked types are to be distinguished. It does not immediately appear which of these represents the more primitive type. Considering, however, the fact that the larvae in which the body skeleton in the first stage forms a basket structure, and which have in their second stage a posterior transverse rod and more or less developed posterolateral processes are characteristic—so far as we know—of the Cidarids, Diadematids and Arbaciids, that is to say of the more primitive forms of Echinoids, it can hardly be disputed that we

have got to regard this larval type as the more primitive form. *Consequently the larval type characteristic of the family Echinidae s. str.*, with the elongated, club-shaped body rods, with the recurrent rod rudimentary or absent, and without a posterior transverse rod or posterolateral processes, *is highly specialized.* It is therefore not at all justifiable to make this larval type represent the Echinoid larva in general as is done in most text-books.

Characteristic of the larval body of the primary type are the vibratile lobes; in the more specialized types, the larva of the Echinidae *s. str.*, and of the Spatangoids, these lobes have disappeared, while the Clypeastroid larvae have retained them to some degree. A further specialization from the lobes are the epaulets occurring in the higher types of the Regularia.

Both the vibratile lobes and the epaulets evidently serve to increase the floating power of the larva. This object is attained to a still higher degree in several larval forms of Regular Echini and Clypeastroids in which muscles connect the lower ends of the rods of the four main arms, so that these arms become actively movable. These larvae, when floating, keep the four main arms in a more or less horizontal position, raising them when disturbed. This is not yet an active swimming movement, the muscular apparatus being too simple for performing regularly repeated movements. Only one Echinoid larva appears to be able to swim actively, viz. the remarkable *Echinopluteus transversus* (of Centrechinidae—H. B. F.), in which a complicate muscular system has developed, the body-skeleton being most extraordinarily adapted for serving as a support to the muscles....

As regards the skeleton it is a noteworthy fact that the fenestrated rods represent a primary structure, as must be concluded from the fact that this type of rods (always confined to the four main arms) is found in the larvae of the more primitive forms....

So far as concerns the broader aspect of this review, a logical conclusion deducible from the array of facts presented is that larval evolution of the echinopluteus must have occurred subsequently to the separation of the main orders and families of echinoids, and within any one group of echinoids the larval evolution has followed similar trends. Thus, within relatively small groupings it is true to say that the young stages of related species show similar ontogenies. It is obvious that, with independent larval evolution occurring simultaneously in the many orders and families of echinoderms in general, the phylogenetic relationship between major groups, such as the classes, will become ever more and more obscured in so far as it is reflected in embryology. The point becomes most important when it is proposed to base relationships between the echinoderm and chordate phyla on evidence obtained from a few selected larval forms which cannot be proved to have any phylogenetic significance. Further discussion of the point must be left to the final part of this article.

3. *Class ASTEROIDEA*

The larva if present in development is, initially at least, always a bipinnaria. A more complex larval form, the brachiolaria, usually follows. The two families Astropectinidae and Luidiidae stand apart from all others in that the larva never, so far as is known, proceeds beyond the bipinnaria stage. All other asteroids appear to possess a brachiolaria, though this may be much reduced in cases of direct development (Mortensen, 1938). Variations in larval development of asteroids, so far as they can be correlated taxonomically, may be summarized in the following way.

Order PHANEROZONIA

Family ASTROPECTINIDAE

The larval forms of five species of *Astropecten* are known with certainty, and all are so similar as to be scarcely distinguishable. Mortensen concludes that the Astropectinidae possess a distinctive larva, which is a bipinnaria having the special characteristics of broad, round anterior lobes. There is no brachiolaria. The larval body is completely absorbed during metamorphosis.

The species studied are: *Astropecten aranciacus* (Metschnikoff, 1885; Hörstadius, 1926); *A. pentacanthus* (Metschnikoff, 1885); *A. scoparius* (Mortensen, 1921); *A. polyacanthus* (Mortensen, 1921, 1937); *A. velitaris* (Mortensen, 1937).

Family LUIDIIDAE

The general characters of the *Luidia* larva appear to be: a more or less pronounced elongation of the anterior part, the median lobes; the total absence of brachiolarian arms and sucking disk. It differs from the *Astropecten* larva by the more developed arms, and the elongation of the median lobes.

Species studied are: *Luidia sarsi* (Meek, 1927; Tattersall & Sheppart, 1934); *L. ciliaris* (Mortensen, 1898, 1913; Gemmill, 1916); *L. savignyi* (Mortensen, 1938).

Other Asteroidea

The remaining families of the Phanerozonia, as well as the other two orders Spinulosa and Forcipulata, possess a brachiolaria or vestige of such a stage.

The following Phanerozonia have been studied: *Pentaceraster mammillatus* (Mortensen, 1938); *Linckia multifora* (Mortensen, 1938); *Asterope carinifera*; *Porania pulvillus* (Gemmill, 1915); *Gymnasteria carinifera* (Mortensen, 1921); *Archaster typicus* (Mortensen, 1921); *Acanthaster planci* (Mortensen, 1931); *Culcita schmiedleriana* (Mortensen, 1931); *Cheiraster gerlachii* (MacBride, 1920); a brachiolaria stage has been established for all of these save the latter species, which is doubtful.

Among the Spinulosa partially direct development, without a pelagic stage, is common. Pelagic brachiolariae are known from the species *Asterina pectinifera* (Mortensen, 1921); *Patiria miniata* (Heath, 1917; Newman, 1925); *Stichaster roseus* (Gemmill, 1916; Mortensen, 1921). In *Asterina regularis* the development has been followed only to the bipinnaria stage (Mortensen, 1921), but no evidence was found to suggest that a brachiolaria stage is omitted. *Brisaster fragilis*, studied by Runnström, is a notable exception to the general rule in possessing large yolky eggs which nevertheless develop into a pelagic larval form, which is a brachiolaria (see below on the relation of egg size to mode of development).

Spinulosa possessing large yolky eggs and having a more or less direct development include species of *Asterina*, *Solaster*, *Fromia* and *Echinaster*, to which reference is made later.

Forcipulata studied include: *Asterias rubens* (Mortensen, 1898; Gemmill, 1916); *A. forbesi* (A. Agassiz, 1877); *A. vulgaris* (A. Agassiz, 1877; Goto, 1896): *Coscinasterias calamaria* (Mortensen, 1921); *Marthasterias glacialis* (Russo, 1892; Mortensen, 1913; Gemmill, 1916). The brachiolaria is the normal larva.

4. *Phylogenetic implications of asteroid development*

The significance of the above facts has been variously interpreted.

MacBride, who regarded the brachiolaria as the more primitive of the two larval forms, considered the sucking disk of the brachiolaria to be homologous with the stalk of an attached pelmatozoon. He regarded the temporary period of attachment in the life of asteroids, followed by the free radial form, as an ontogenetic recapitulation of the evolutionary history of the class.

In opposition to the above view Mortensen (1921) pointed out that the brachiolaria larva is restricted to the more specialized Asteroidea (i.e. the Spinulosa and Forcipulata) while the more primitive Phanerozonia lack the larva (the fact that Phanerozonia such as *Archaster* possess a brachiolaria being unknown at that date). He also considered that the brachiolarian arms and sucking disk are essentially specialized structures, the more so since they arise relatively late in development, subsequent to the bipinnaria stage. He considered the bipinnaria to be the primitive form, and that phylogenetic speculations based on brachiolarian structures cannot be held valid.

MacBride (1921) in reply stated his belief that the Spinulosa, not the Phanerozonia, are the more primitive asteroids, and he explained the absence of an attached stage in the Phanerozonia as consequent upon sandy or muddy habitats not permitting such a stage. In the former contention MacBride is not supported by the majority of taxonomists of the group.

W. K. Fisher, H. L. Clark, R. Koehler and L. Doderlein all agreed that the Astropectinidae are most primitive. MacBride and Perrier were alone in regarding the Spinulosa as occupying this place. Gemmill (1923) stated that he did not regard the Astropectinidae as primitive, and considered that the Asterinidae should be placed in the Phanerozonia. The latter opinion, of course, is again contrary to the views of most taxonomists.

Bather (1923) gave it as his view that, assuming Mortensen to be correct in asserting that only the more specialized forms possess the sucking disk, the sucker may none the less perpetuate ancestral structure.

MacBride in 1923 repeated his opinion that the crinoid larva and brachiolaria are comparable: in both there occur the long preoral lobe, ventral stomodaeum, right and left posterior coeloms. In both the preoral lobe becomes the stalk. He regarded the stalk as homologous in each case.

Hörstadius (1926), following his study of the development of *Astropecten*, considered that the bipinnaria is more primitive than the brachiolaria.

Mortensen (1931), after his discovery of the brachiolaria in *Archaster* and *Acanthaster*, restated his views as follows:

We know now the Brachiolaria to be the more generally occurring type, the true Bipinnaria being known to occur only in *Astropecten* and *Luidia*, whereas the Brachiolaria is known to occur in *Archaster*, *Acanthaster*, *Asterina*, *Porania*, *Asterias*, as also the *Solaster* larva must be regarded as a reduced Brachiolaria. This fact might perhaps speak for the Brachiolaria being the original type, as is the opinion of MacBride. Still, the fact that all the larvae pass through a typical Bipinnaria stage, before reaching the Brachiolaria stage, is decidedly in favour of regarding the more simple Bipinnaria as the primitive type; so too is the fact that the simple Bipinnaria is peculiar to the *Astropectinids* which are generally regarded as the more primitive type of Asteroids.

One fact appears certain. Larval evolution has occurred to a considerable degree in the Asteroidea, though not along channels markedly correlated with adult taxonomy. Mortensen's contention that phylogenetic speculations based on the larval structure are unjustified appears to be the inevitable conclusion.

III. DIRECT DEVELOPMENT IN ECHINODERMS

1. *Incidence*

Until recently it had come to be generally assumed that all typical echinoderms have an indirect mode of development; whenever an echinoderm had been found to depart from this criterion it had commonly been glossed over as atypical. In 1945 I drew attention to the fact that this belief is not supported by available evidence. On the contrary, a survey of the known embryological data of particular faunas indicates that no special mode of development can be taken as the general rule for the phylum.

There are some sixty-one British echinoderms about which sufficient information is available to show, with a reasonable degree of certainty, the type of development followed. Of these, direct development of some kind or other probably occurs in 70% of the Holothuroidea, 63% of the Asteroidea, 25% of the Ophiuroidea, 14% of the Echinoidea, and apparently in all the Crinoidea. Among the New Zealand Ophiuroidea, 63% of the species about which any embryological knowledge is available probably have a more or less direct development. Of the Antarctic ophiuroids studied by Mortensen (1936), there are some fifty-six species whose development is known in part, or which can be deduced with probability, and 70% of these appear to have a direct development. No doubt similar evidence would be provided by other faunas. It is clear that the notion that echinoderms normally have an indirect development, with pelagic larval stages, cannot be maintained. Rather, it would appear that the particular kind of development followed depends on particular conditions obtaining in each species—conditions which can be analysed with some measure of success.

2. *The origin of direct development*

In my opinion the causes of direct development are closely related to the physical characters of the ovum (Fell, 1945). The Ophiuroidea can conveniently be grouped into three major categories according to the nature of their ontogeny. These

categories, of course, have no phylogenetic significance, and cut across natural taxonomic groupings.

Group 1 includes ophiuroids with small eggs (not greater than 100 μ in diameter), such as *Ophiothrix* and *Ophiocomina*. The egg is deficient in yolk and the cytoplasm is not abundant. They have the common character of undergoing a long, indirect mode of development, involving a well-formed pelagic ophiopluteus, followed by a pronounced metamorphosis. Group 2 includes ophiuroids with eggs of intermediate size (between 100 and 300 μ approximately), and in which there is a moderate quantity of yolk material. The yolk (as also the cytoplasm) can be measured by fairly accurate means, and in a typical case is equal to $8{\cdot}8 \times 10^4$ cu.μ. Examples are *Amphipholis squamata* and *Ophioderma brevispina*. These exhibit intermediate stages in the nature of the development, which involves a non-pelagic non-feeding larva of a variable degree of simplicity, sometimes vestigial. Group 3 includes ophiuroids with large, yolky eggs (from 400 μ upwards). Here the yolk and the cytoplasm are abundant, the yolk in a typical case measuring $5{\cdot}3 \times 10^6$ cu.μ, thus exceeding that of Group 2 by some sixty times. The cytoplasm also reaches the relatively high value of 92% of the volume of the entire egg. The mode of development is absolutely direct, without trace of a larval stage. Typical species are *Ophiomyxa brevirima*, and Kirk's ophiuroid (the specific identity of the parental form being yet in doubt). Thus with increasing egg size there is associated a steadily increasing tendency to undergo direct development.

The increase in yolk does not greatly modify the process of cleavage, as segmentation in most forms is total. In *Amphiura vivipara*, however, according to Mortensen (1921), a blastoderm forms on the animal hemisphere. In all cases where yolk is abundant there is at least a tendency to form micromeres and macromeres. Embryos of Group 1 have a symmetrical blastula with a large central blastocoel. In Group 2 the wall of the blastula is thick and the blastocoel tends to be mainly in the animal hemisphere. In Group 3 the blastocoel is reduced to a vestigial meniscus-shaped cavity in the animal hemisphere, while the wall of the blastula is greatly thickened by yolk-laden cells arranged compactly; the wall is several cells thick. The mesenchyme fails to separate as such, but remains as a great bulging mass projecting upwards into the blastocoel. The reduction of the blastocoel has a profound effect on gastrulation.

In the non-yolky embryos of Group 1 gastrulation is effected by invagination from the vegetal pole. The result of yolk in the other groups is, first, to reduce invagination to a solid inpushing of mesenchyme cells; secondly, to bring about a subsequent immigration of micromeres to contribute to the mesendoderm. The archenteron in Group 3 is thus vestigial; it disappears, giving rise to no definitive structure. The enteron is later excavated by a process of splitting in the mesendoderm. In this case the vestige of the blastopore becomes the mouth, whereas in Group 1 it gives rise to the anus. Thus the distinction between mouth and anus in regard to their mode of development is not a significant one.

At this point in development there is a still wider parting of the ways in the various groups. The heavily-yolked embryos proceed to adopt radial symmetry, whereas the

others become bilaterally symmetrical. The apparent hiatus between the two categories, is, however, illusory, as is apparent from the following considerations.

3. *Recession of metamorphosis and the loss of larval form*

To account for the change from indirect to direct development, with consequent elimination of the bilaterally symmetrical stage, I have suggested that with an increasing yolk mass there has been a tendency for a backward shift in time of the

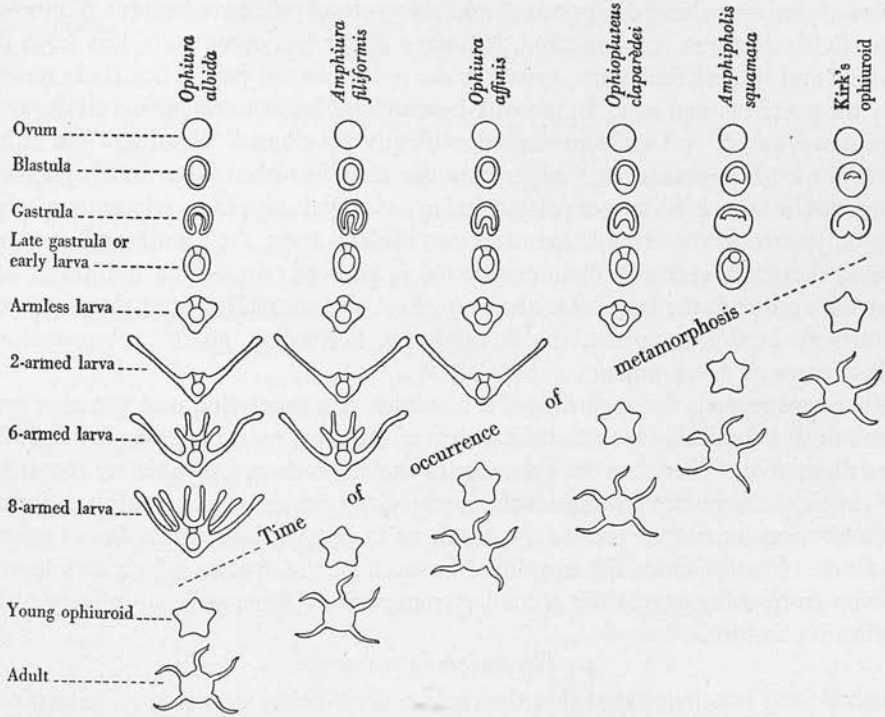

Fig. 6. Diagram illustrating the theory that metamorphosis in ophiuroids has tended to undergo a backward recession towards the gastrula stage.

point at which radial symmetry is adopted, a concept termed 'recession of metamorphosis' (Fell, 1945). The essential features of this hypothetical process are illustrated in Fig. 6 (it should be noted that the blastula and gastrula of *Ophiopluteus claparèdei* are still unknown, so that their nature has had to be deduced by interpolation). It is envisaged that with the evolution of yolk the backward shift of the time of metamorphosis has operated so as to remove from development in succession one ontogenetic stage after another, with an end-point in forms where the gastrula itself 'metamorphoses' into a radial form.

If this theory of receding metamorphoses be true, it is reasonable to expect in nature a bioseries illustrating transitional stages. A survey of ophiuroids shows that

such does in fact exist, and no doubt similar bioseries will be found in the other echinoderm classes.

Fig. 6 shows a series of adult ophioplutei, i.e. larvae which have reached the point in development at which metamorphosis is imminent. In the fully developed ophiopluteus, as exemplified by *Ophiura albida*, the full complement of four pairs of larval arms is present, each supported by a skeletal rod. There is a functional alimentary canal, with stomodaeal oesophagus and proctodaeal intestine leading to the mouth and anus respectively. *Amphiura filiformis* has an ophiopluteus in which the posterodorsal arms have disappeared, and the postoral pair have become reduced in size. Other features are unaltered. *Ophiura affinis* has completely lost both the postoral and anterolateral arms, as well as the posterodorsal pair. Thus there remain only the posterolateral pair. In the yolk-bearing *Ophiopluteus claparèdei* all the arms have disappeared, and are represented evidently by ciliated 'shoulders' on either side. A mouth is present but apparently the anus has been lost. In *Amphipholis squamata* the larva is no longer pelagic, being a vestigial stage in a viviparous species. The only trace of the arms is found in two skeletal rods, the mouth and anus are absent, though a vestigial alimentary canal is present. In Kirk's ophiuroid and *Amphiura vivipara* the larval stage has vanished. We are really witnessing a process of neoteny in this sequence, the larval forms becoming 'adult' at successively earlier stages of development.

There are reasons for regarding the bioseries as a regression and not as a progression. It is improbable that skeletal rods of the arms would arise earlier than the arms themselves. Therefore the existence of skeletal rods in *Ophiopluteus claparèdei* and *Amphipholis squamata* indicates the vestigial, not primitive, nature of these forms. A closed non-functional alimentary canal, as in *Amphipholis*, must be a vestigial condition. Finally, since the simplified larvae, and the species which lack larvae, develop from yolky eggs, their secondary nature is evident; yolk is unlikely to be a primitive feature.

4. *The coelom in ontogeny*

It had long been supposed that the coelom of all echinoderms is an enterocoel; one, that is, which arises from paired pouches nipped off from the archenteron. There can now be no doubt that a schizocoel is often present in echinoderms, and probably nearly always occurs in forms with yolky eggs. The various modes of development of this complex system of cavities lined by epithelium may be very briefly summarized by reference to the three main ontogenetic groups of ophiuroids.

In *Ophiothrix*, representing Group 1, MacBride records that right and left enterocoels form. The left divides into anterior and posterior parts, and soon afterwards the right does so also. From the posterior wall of the left anterior coelom the hydrocoel arises. The wall of the left posterior coelom forms the arms, and its wall the general perivisceral coelom. The right coeloms become vestigial. Other complexities reported by MacBride have since been stated to be a misinterpretation (Narasimhamurti, 1933).

In *Amphipholis*, representing Group 2, I have recorded structures in the vestigial

larva which can be homologized with right and left enterocoels, but these arise by schizocoelous splitting within solid masses of mesendoderm on either side of the enteron (Fell, 1946). Occasionally a small posterior pouch is found. The right pouch, and the posterior one if present, soon disappear, and contribute to the general mesoderm, but the left pouch survives to form the five-lobed hydrocoel in the usual way. The general perivisceral coelom and other accessory parts of the coelom, all arise much later in the radial form by schizocoelous splitting in mesenchyme. In Group 3, represented by Kirk's ophiuroid, the entire coelom is formed by splitting in mesenchyme (Fell, 1941). There is a period when the free-living young ophiuroid has no general body cavity, as the perivisceral coelom forms quite late in development. A similar condition appears to hold in *Ophiomyxa brevirima*.

5. *Causes of direct development*

It may be regarded as reasonably proven that the accumulation of yolk and cytoplasm in the egg is in some way responsible for suppression of the larval form. The salient features of the sequence of reduced larvae studied above are: first, a progressive reduction in size and number of the paired larval arms, followed by loss of the arm skeleton; secondly, an increase in the amount and importance of mesenchyme, within which ultimately the coelom is excavated in place of coelomic pouches from the enteron; finally, there is complete loss of bilateral symmetry. The order in which these reductions occur, in terms of increasing yolk mass, suggest progressive inhibitions in metabolism along the axes of a bilaterally symmetrical body.

Child in 1916 showed that a wide range of simple chemical substances could cause an inhibitory effect very similar to those noted above. He was able to produce echinoplutei showing successive degrees of reduction and obliteration of antero-posterior, medio-lateral and apico-posterior differences through inhibitions of the axial metabolic gradients. In extreme cases his larvae resembled the peculiar armless larvae which we now know to develop from yolky eggs. Child drew the inference that echinoderm larvae may have been evolved by increases in metabolism along the metabolic gradients, producing the outgrowth of paired arms, etc. I have suggested that a reversal of the process would account for the regression series, and that the associated yolk material may have been the inhibitory agent (Fell, 1945). It must be conceded, however, that the apparent chemically inert character of yolk material makes it improbable that it could act in a manner strictly comparable with a simpler substance. There are further parallels. Child found that mesenchyme was unaffected by the inhibitory influences, and underwent a great increase at the expense of the bilateral organs. The same increase in mesenchyme is seen in relation to loss of bilateral organs in embryos derived from yolky eggs. Successive loss of bilateral organs implies an effective shift of metamorphosis towards the gastrula stage; the bilateral organs—the essential features of an echinoderm larva—gradually cease to intervene between the gastrula and the final form.

6. *Phylogenetic implications of direct development*

The phenomena associated with direct development serve yet again to emphasize the unreliability of larval forms as evidence of phylogenetic relationships. In these cases evolution has affected the larva so as to bring about its degeneration and eventual disappearance, while the adults retain all the features of echinoderms quite unaltered. The coelom of an adult *Ophiomyxa* shows no significant difference from that of an adult *Ophiothrix*, yet the modes of origin of the structure are entirely different in the two cases. The coelom is evidently subject to severe alterations in its mode of development. In deducing supposed relationships between hemichordates and echinoderms, certain similarities between the embryonic coelom of selected larvae have been much stressed as important evidence. When it is considered how variable the coelom can be in regard to its embryological origin and initial form, the validity of any phylogenetic importance attached to its ontogeny becomes extremely dubious.

IV. VIVIPARITY IN ECHINODERMS

Viviparity is of interest in echinoderm reproduction owing to the modifications of development which usually accompany its occurrence. It is commonly the case that eggs of viviparous species are large and yolky. The relationship between the parent and young is often extremely intimate, with marsupia forming in the mother, an embryonic attachment developing, and even nutritive substances sometimes being supplied to the embryo by the parent. Larval stages are vestigial or suppressed altogether.

Among asteroids simple brood-protection is illustrated by *Calvasterias suteri*, known from the sub-antarctic islands of New Zealand. The eggs are laid, and the numerous young are carried, in a large cluster about the mouth, apparently in the later stages living as commensals. In the astropectinid species *Leptoptychaster kerguelensis* Sladen (1889) reports that the young stars are hatched in the oviducts and later adhere to the re-entrant angles between the rays of the parent. *Leptasterias groenlandica* is reported by Lieberkind (1920) to hatch its young in its stomach, a very surprising circumstance with interesting physiological possibilities. In species of *Echinaster* the young are carried in the ambulacral grooves with the sides of the arms folded over them. More complex conditions are seen in *Pteraster* and *Hymenaster* where there occurs a complex dorsal marsupium, held up by modified paxillae, and opening dorsally by a special osculum. A marsupium is known also in *Granaster nutrix*. In the starfish *Asterias spirabilis* the embryo is joined to the parent by an attachment.

In ophiuroids all degrees of brood protection and viviparity are found; the condition is very common in antarctic species, of which Mortensen (1936) has recorded thirty-one as viviparous. A very interesting case has been recorded in Britain by Smith (1938) who found numerous young individuals of *Ophiothrix fragilis* clinging

to the spines and tube-feet of adults, larger young ones occurring separately in the parental bursae. As this species has non-yolky eggs and well-developed pelagic larvae, this is an unexpected case and indicates how viviparity might arise in such forms. Smith regards the case as equivalent to natural crevice sheltering. In truly viviparous ophiuroids the eggs are usually large, and either many young may be found in the bursa, as in the New Zealand species *Ophiomyxa brevirima* (Mortensen, 1924; Fell, 1941*a*); or several, as in *Pectinura cylindrica* (Mortensen, 1924; Fell, 1941*a*); or only a few, as in *Amphipholis squamata* (Fell, 1946). The last-mentioned species, as others of the same genus, is notable in having an embryonic attachment to the parent. This structure is not nutritive; reasons have been given for believing that a nutritive fluid is secreted by the bursal wall, a conclusion supported by experimental culture of embryos *in vitro*, when it is found that the latter require chemical additives in order to develop normally (Fell, 1940*b*).

In comatulid crinoids, where the eggs are large and rich in yolk, it is the general rule for the young to adhere to and develop on the pinnules of the parent. In some species, however, the eggs are free, as for example *Tropiometra carinata* and *Antedon petasus* (Mortensen, 1921). True viviparity, involving special marsupia, is found in antarctic crinoids such as *Isometra vivipara* (Andersson, 1905; Mortensen, 1920), and *Thaumatometra nutrix*. In *Notocrinus virilis*, also, Mortensen (1921) records marsupia, and it appears that in this species the young are nourished by an albuminous secretion from the wall of the marsupium.

Similar degrees of brood protection and of viviparity are to be observed in the holothurians, where the incidence in antarctic species is as pronounced as in the other classes. In the simplest type the embryos merely rest on the surface of the body. In other species small alveoli may form in the integument, enclosing the eggs. Sometimes the eggs develop within the oviducts, or within the coelom. In other cases an invagination or evagination of body wall will form a marsupium. Genera showing viviparity include *Cucumaria*, *Thyone*, *Psolus* and *Phyllophorus* among Cucumariidae, and *Chiridota*, *Synaptula* and *Leptosynapta* among Synaptidae.

Since echinoids are distinguished from other echinoderms by possessing generally small eggs and pelagic larvae, viviparity is necessarily of limited incidence in the class. Among cidarids Mortensen (1926) has shown that the New Zealand *Goniocidaris umbraculum* carries the young in the partly sunken peristome, covered over by oral spines, thus forming a marsupium. In other cidarids the spines of the apical part of the test form a marsupium. Among the spatangoids the sunken petals frequently serve as marsupia, as in *Schizaster*, *Hemiaster* and others. In some species sexual dimorphism of the test is a consequence of this condition.

It is clear that brood protection and viviparity can influence development considerably. Larval stages can be effaced or at least reduced. New embryonic organs may evolve, such as the attachment stalks between embryo and parent. New modes of nutrition may arise, involving a change from ingestion of planktonic food in a functional alimentary canal to surface absorption of fluid material by the outer epithelia of the embryo. Yet in these cases the end result is the same—an adult

echinoderm arises quite as typical of its group as an oviparous form. Here, then, is just one more illustration of the potency of evolution in acting upon embryonic stages without significantly affecting the adult.

V. ECHINODERM EMBRYOLOGY AND THE ORIGIN OF CHORDATES

The foregoing survey has attempted to collect together the salient features of echinoderm embryology which can have any bearing on the phylogenetic inter-relationships of the several classes within the phylum, as well as on the wider problem of whether there is any relationship between the echinoderm and chordate phyla. The conclusion appears to be inevitable that intolerable discrepancy exists between phylogenetic inferences drawn on the basis of the recapitulation theory and those drawn from comparative morphology and palaeontology. Each of the two opposed sources of evidence, if utilized to construct a hypothetical phylogenetic tree, provides a result absurdly different from the other. In illustration, let it be assumed that both approaches to the problem are legitimate. The two contrasting results will then be reached on lines somewhat as follow.

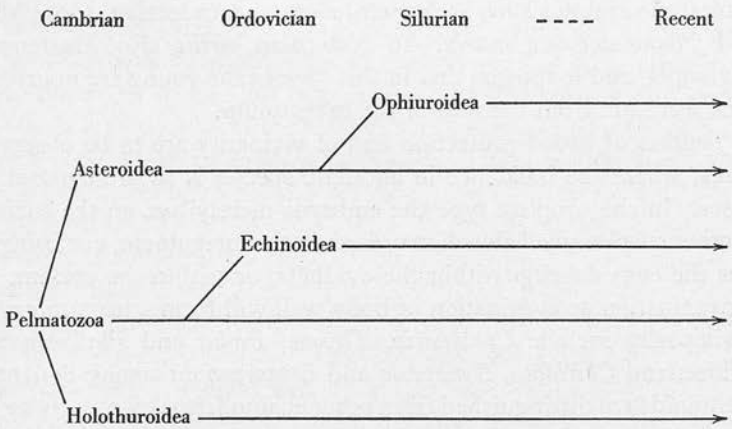

Fig. 7. Apparent relationships of echinoderm classes as suggested by morphological and palaeontological evidence.

Fig. 7, while in no way intended to represent established fact, indicates very approximately the kind of phylogenetic relationships between the extant classes of echinoderms and fossil species which morphology and palaeontology suggest. Already in Cambrian times Pelmatozoa, Holothuroidea and Asteroidea had become distinct groups. Morphology suggests that the two latter arose from the Pelmatozoa. Echinoidea, which appear in the Ordovician, seem to have arisen directly from Pelmatozoa. Ophiuroidea appear in the Silurian, and fossil evidence leaves little doubt that they arose from the asteroid stem—a conclusion which comparative morphology also supports. There is no fossil evidence to suggest any connexion between echinoderms and the chordate stem.

Fig. 8 represents the kind of phylogenetic tree which the recapitulation theory would construct from embryological evidence, if larval forms are regarded as repeating ancestral conditions. A common dipleurula ancestor gave rise to three stems. The first led to the Pelmatozoa, the other two led to a pluteus and an auricularia respectively. Later the pluteus ancestor gave rise to ophiopluteus and echinopluteus forms, and these led to the Ophiuroidea and Echinoidea respectively. The other line, the auricularia, gave rise to three forms. One of these, a pentacula, led to the Holothuroidea. Another was the bipinnaria, which led to Asteroidea, with a possible anchored brachiolaria ancestor intervening in some groups as a recapitulation of the original Pelmatozoan stalked stage. The remaining descendant was a tornaria, the ancestor of the Hemichordata, and, by assumption, of all other chordates. The vitellaria larva, the pupa of crinoids, and the other larval forms fail to fall in line with the foregoing, and have to be relegated to the status of 'caenogenetic structures'.

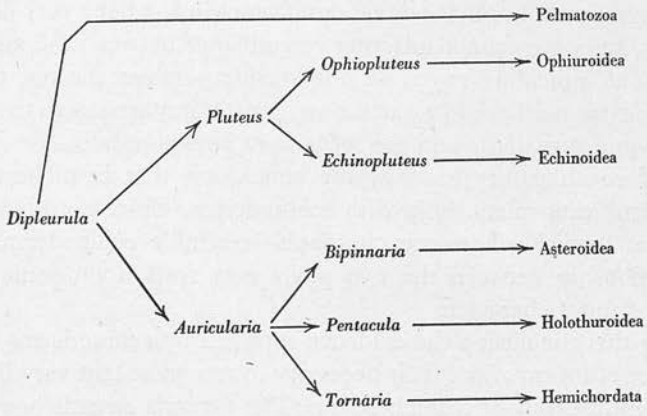

Fig. 8. Apparent embryological relationships of echinoderms and hemichordates.

The second account, based on the supposition that larval forms retain ancestral structure, is grossly opposed to what all other evidence would lead us to believe are the relationships between echinoderm classes. It is impossible to accept the result which implies that ophiuroids and echinoids are more closely related to each other than to the other classes, and that holothurians and starfish are similarly connected. If, therefore, the recapitulation theory as applied to larval forms leads to a *reductio ad absurdum* in the case of echinoderms alone, the result can only be regarded as equally unsatisfactory in regard to the supposed chordate connexion, for which there is no other palaeontological or morphological evidence.

Manifestly, evidence from these larval stages is not susceptible to inductive reasoning on the basis of their being recapitulated ancestral stages. The reason for this has become clear now that the extremely variable nature of the echinoderm larva is known to be one of its chief attributes. The position appears to be analogous

to the *impasse* arrived at some years ago in connexion with the taxonomy of digenetic trematodes. Widely divergent phylogenies were proposed by various workers, according to whichever particular larval characters were regarded as significant. Later, however, the stability of the excretory organs was established, and a more satisfactory classification developed. In the echinoderm larvae there seems to be no comparably static larval organ. The nearest approximation is found in the ciliated band, but even this is stable only during the initial dipleurula stage.

This survey has shown how, in each of the various fields chosen for particular examination, variation of the larval form can occur, often resulting in wide divergence within small groups, and equally often resulting in surprising convergence between distantly related groups. Since larval variation of a profound extent can be observed in particular cases, it becomes highly probable that the same is true of other cases where the point cannot yet be proven so clearly. Thus there is every reason to accept Mortensen's view that the characteristic echinoderm larval forms are specialized stages, without phylogenetic significance in any but a very limited extent. Consequently, since we cannot interpret resemblance between the auricularia and the bipinnaria as indicating any close relationship between the two classes which possess these larvae, neither can we attach any greater importance to the resemblance between the same auricularia and the tornaria of hemichordates.

It is therefore obligatory to draw the conclusion that hemichordates do not exhibit any significant relationship with echinoderms. Since no other chordates—supposing that hemichordates are chordates—resemble echinoderms, the whole assumed relationship between the two phyla now rests upon some biochemical evidence of a slender character.

In reaching this conclusion the evidence supplied by echinoderms has not been the only source of information. It is necessary to recognize that very little is known as yet of the embryology of hemichordates. The tornaria larva is one about which no wide body of data is available; comparative embryology does not yet exist within the hemichordates in the sense that it does in echinoderms. Not all hemichordates possess a tornaria. Although the complete embryology of the New Zealand *Dolichoglossus otagoensis* has not yet been worked out, it is certain that no tornaria stage occurs in its life history. The embryo proceeds to adopt the adult form without any pelagic larval stage (Kirk, 1939). It is therefore clear that evolution has operated upon the embryonic stages of at least one hemichordate in much the same manner as it has in echinoderms.

Clark (1937) has been forced to the conclusion that the various animal phyla arose independently. In regard to the topic here discussed he writes (private communication, 1945): 'The whole subject is complicated by the undependability of the evidence afforded by the larval stages. We need to know far more about the ecology, so to speak, of larvae than we do now. Larvae seem to be as much subject to adaptation to their surroundings as are the adults, at least in many groups. . . . There is no doubt that the echinoderms are all closely related; but the relationship is to be sought only in the very early stages, no later than the late gastrula. Thus I do not

believe that the vertebrates were derived through the echinoderms'. Although perhaps a majority of workers is still inclined to regard the dipleurula larva as recapitulating a common ancestral form of existing echinoderms, in his main conclusion Clark receives strong support from the facts now known about echinoderm embryology.

VI. SUMMARY

1. Development in echinoderms may be indirect, involving pelagic, bilaterally symmetrical, larval forms, or more or less direct, with the larval stage either reduced or omitted. Of the five living classes, only the Echinoidea are characterized by being predominantly of the type with indirect development.

2. It is possible to regard the dipleurula stage of the classes Asteroidea, Ophiuroidea, Echinoidea and Holothuroidea as recapitulating a common ancestral *Dipleurula*. It is no longer possible to regard any of the other types of echinoderm larvae as anything but specialized forms without broad phylogenetic significance.

3. Embryos and larvae of echinoderms are extremely plastic, often exhibiting convergence, divergence and adaptation, susceptible to evolutionary modifications of structure which may act quite independently of the adult stage. Ancestral structure cannot be deduced from such forms.

4. In the Echinoidea larval evolution seems to have occurred subsequently to the separation of the main orders and families. Within relatively small groups larval evolution has followed similar trends, so that characteristic larvae occur in various sub-groups, where the young stages may follow similar ontogenies; but such independent evolution tends to obscure the phylogenetic relationships between the class as a whole and the other classes.

5. In the Asteroidea larval evolution has occurred along channels not so markedly correlated with the taxonomy of the adults. Phylogenetic speculations based on such larval stages prove incompatible with other evidence.

6. In the Holothuroidea and Ophiuroidea larval evolution cannot at present be related with adult taxonomy, save in one or two cases too unimportant to have general significance.

7. The egg of echinoderms is liable to undergo changes in volume. Increase of volume is directly related to increase in cytoplasm and its product, the yolk material. Such increases have led to direct development.

8. Increase in cytoplasm and yolk has not greatly affected the cleavage process, which is almost always total. A distinction between micromeres and macromeres frequently results.

9. With increasing cytoplasm, the wall of the blastula becomes thicker, and the blastocoel is in extreme cases reduced to a vestige in the animal hemisphere. The mesenchyme fails to separate as such, but projects as a solid mass into the blastocoel. Invagination is reduced to a solid inpushing of cells, and epiboly may ensue. The archenteron may become vestigial, in which case the definitive enteron is excavated in the solid endoderm by splitting. The enterocoele become reduced or lost, and the coelom and its adjuncts may arise by schizocoelous splitting in mesenchyme.

10. In Ophiuroidea a succession of stages in reduction of the ophiopluteus may be seen, suggesting a recession backwards in time of the moment at which metamorphosis is initiated. In extreme cases the gastrula itself becomes radially symmetrical and the larva is completely lost.

11. By convergent evolution among echinoderms with yolky eggs, a special vitellaria larva has arisen independently in Holothuroidea, Ophiuroidea and Crinoidea. The

vitellaria is characterized by its barrel shape, and the transmutation of the ciliated band into annuli. In the Crinoidea this is the only larva as yet known.

12. Viviparity does not seem to have been an important factor in causing direct development, though it may influence the physiology and morphology of the young stages.

13. If larval stages of echinoderms are interpreted as recapitulating ancestral stages, the conclusions reached are seriously discordant with other evidence. Therefore it is not possible to base phylogenetic interpretations on larval stages alone.

14. Echinoderm embryology cannot provide any valid support for the hypothesis that chordates arose from echinoderms.

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Research Notes

New Zealand Fossil Asterozoa
3. *Odontaster priscus* sp. nov. from the Jurassic

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[*Read before Wellington Branch, April 28, 1954; received by Editor, March 29, 1954.*]

Abstract

Odontaster priscus sp. nov. is described from a Temaikan horizon (Bajocian-Bathonian) near Onewhero, South Auckland. The generic determination is based on ambulacral peculiarities which are considered to be diagnostic of *Odontaster* sensu lato.

Order Phanerozonia
Family Odontasteridae
Genus Odontaster Verrill 1880
Type species *Odontaster hispidus* Verrill

Odontaster priscus sp. nov.

Holotype (Figs. 1 and 2)—an internal negative mould in medium sandstone of the coelomic surface of the adoral body-wall. It was collected by Miss Helen McKenzie from Moewaka Quarry, Opuatia Stream, Onewhero Survey District, Geological Survey locality G.S. 5037, and through the courtesy of Dr. C. R. Laws is now in the N.Z. Geological Survey collection, specimen EC. 184. Marwick (1953, p. 126) considers the horizon to be Temaikan, about Bajocian or Bathonian.

Of small size, R estimated to be 11.0 mm., r about 3.5 mm. Disc evidently stellate, tapering evenly into the arms. Distal parts of arms lacking, but apparently acuminate.

A ring of five pairs of large, elliptical skeletal plates surrounds the mouth, one pair at the proximal end of each ambulacral series. Each plate is about 1 mm. in length, with the major axis directed radially, and the better preserved ones have the upper surface concavely excavate and traversed by three or four transverse ridges. The relationship of these structures to one another and to the ambulacral series and to the mouth can best be understood by reference to Fig. 2, which is to be treated as the essential diagnosis of the species.

Discussion

Until the discovery in August, 1952, of this problematic fossil no Jurassic asteroid was known from New Zealand. Although identification appeared at first sight almost hopeless, the unusual character of the five pairs of radially-placed ridged plates around the mouth seemed to offer a chance of success. It was first assumed that the mould was a negative impression of the adoral lower surface, and that the grooved plates were therefore oral plates. A few genera, such as *Archaster*, have very large oral plates, but their detailed sculpture differs, and it was difficult to understand why the plates in the fossil were grouped in radial pairs instead of interradial pairs, as is universally the case. Furthermore, the lack of any impression of inferomarginals was puzzling, and seemed to point rather to some non-phanerozonian genus, in which case the large size of the oral plates seemed anomalous. The alternative interpretation was therefore tried, namely that the specimen is a negative impression of the internal adoral surface, such as would result from the percolation of sand and mud into the coelomic cavity after decay of the aboral surface of the disc. On this assumption the grooved plates would be some peculiar development of the ambulacral series of ossicles. This would account for their radial position and for their relatively greater distance from the mouth impression than should be the case with oral plates. It would also explain the lack of any impress of marginal plates. Since internal skeletal structures of asteroids are seldom mentioned in

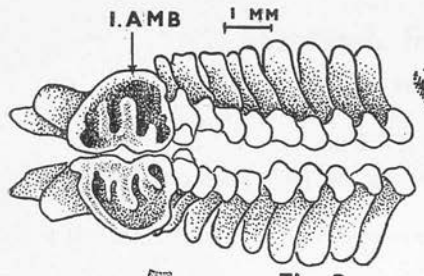

Fig. 3

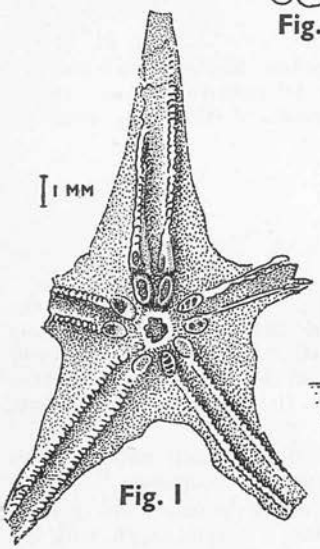

Fig. 1

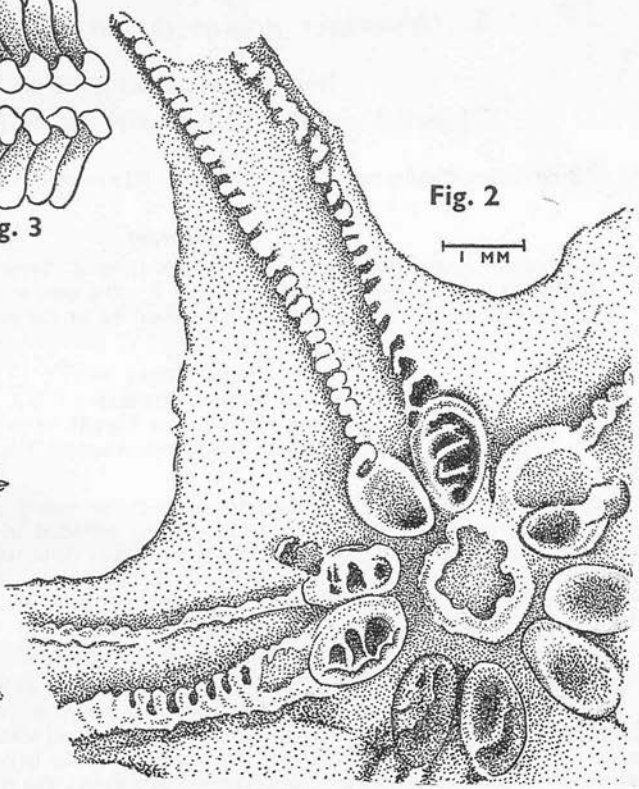

Fig. 2

Figs. 1 and 2—*Odontaster priscus* sp. nov. holotype. Fig. 3—ambulacral ossicles in *Odontaster meridionalis* (Smith), seen from above in a specimen of R 40 mm. 1 AMB, enlarged first ambulacral. Figs. 1 and 2 are drawn from positive plasticine presses made from the original negative natural mould.

systematic diagnoses, it was necessary to dissect a series of representative genera in order to discover whether skeletal plates of the type noted occur in any of them. Analogous structures were found in a specimen of *Odontaster meridionalis* (Smith), from Heard Island. In this species the first pair of ambulacral ossicles is much enlarged, and each plate carries on its upper surface several transverse grooves and ridges which traverse a concave depression; Fig. 3 illustrates the condition in a specimen of major radius 40 mm. Reference to Fisher (1911) shows that he had noted similar structures in *Odontaster crassus*. He writes (p. 157): "The enlargement of the first pair of ambulacrals with the accompanying development of the dorsal transverse muscles is undoubtedly connected with the movement of the combined mouth plates. These, being angular, almost completely close the actinostome, and the small marginal spines completely close the opening . . . The enlargement of the first pair of ambulacrals is abrupt, and so noticeable as to form a good generic character. The same enlargement occurs, but in a lesser degree, in *Asterodon singularis* (Mueller and Troschel)."

Evidently the grooved and ridged radial plates in the Onewhero fossil are similarly enlarged ambulacral plates. Dissected specimens of *Asterodon miliaris*, *A. robustus* and *A. dilatatus* were found to show a weak development of the same type but, as Fisher found in *A. singularis*, the ambulacrals are not nearly so strongly enlarged as in *Odontaster*. Both *Asterodon* and *Odontaster* are placed in the family Odontasteridae. It is therefore concluded

that some tendency towards enlarged and ridged first ambulacrals is a familial character of the Odontasteridae, but is fully expressed in *Odontaster* only. Accordingly the Onewhero fossil is referred to that genus, sensu lato.

A second fragmentary impression of a starfish of the same size as the holotype occurs on the same slab. It is an external mould, and the impressions of marginal plates can be seen on one arm. There is no reason to doubt that it is the same species. *Odontaster*, like *Asterodon*, is a southern circum-polar genus in existing seas, and is restricted to colder temperate and sub-antactic waters. However, before *Odontaster priscus* can be utilized in zoogeographic studies one will need to know whether it exhibits the other diagnostic features of *Odontaster* sensu stricto.

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AN ECHINOID FROM THE TERTIARY (JANJUKIAN) OF SOUTH AUSTRALIA
BROCHOPLEURUS AUSTRALIAE sp. nov.

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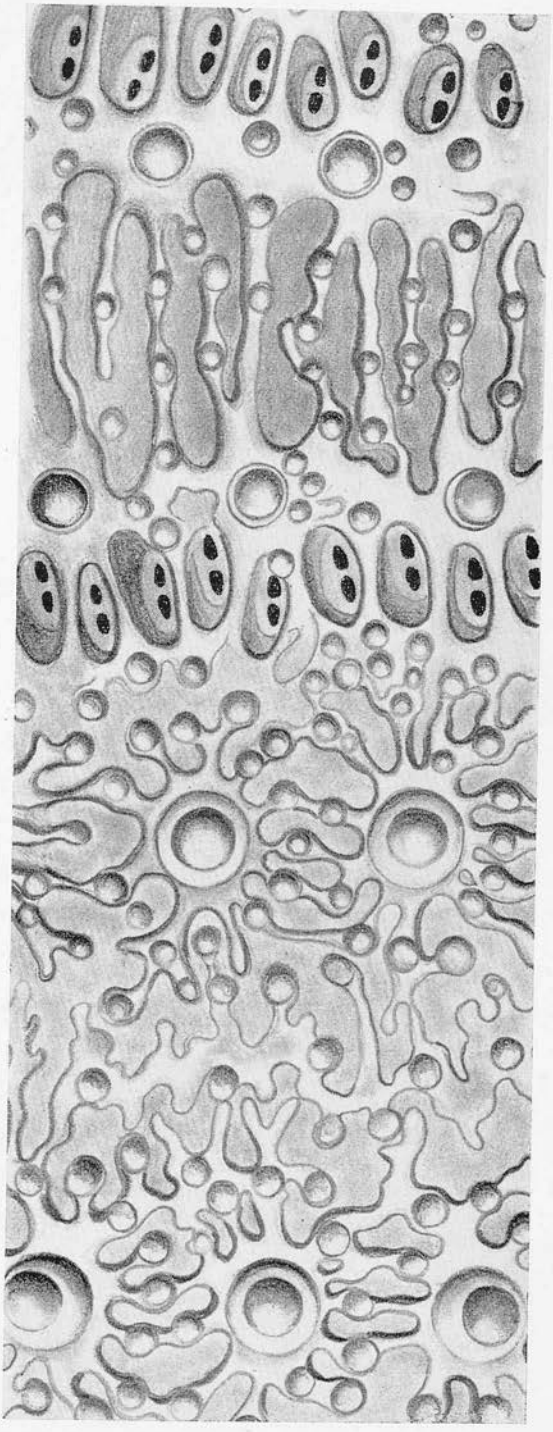
Reprinted from Memoirs of the National Museum, Melbourne
No. 16

ISSUED DECEMBER, 1949



Brochopleurus australiae, sp. nov., holotype.
Ambulacrum and interambulacrum, near ambitus, to show detail of sculpture.
Magnification ×48.

AN ECHINOID FROM THE TERTIARY (JANJUKIAN) OF SOUTH AUSTRALIA

BROCHOPLEURUS AUSTRALIAE sp. nov.

By H. Barraclough Fell,
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Plate I.

(Received for publication October 13, 1948.)

Through the courtesy of the National Museum of Victoria, a collection of Australian Tertiary Echinoids was lent to me for comparison with similar material from New Zealand. The results of this will be published later, but, in the meantime, it is desirable to record an undescribed species included in the collection of the Museum which has been confused with *Paradoxechinus novus* Laube (1869). The species is referable to *Brochopleurus* Fourtau (1920), which genus differs from *Paradoxechinus* in a number of respects, the chief being that, in the former, the primary tubercles are each surrounded by a distinct radiating sculpture, whereas in the latter there is no such radiating sculpture, the primary tubercles being joined to their neighbours by straight lines of raised sculpturing, forming therefore a zig-zag line along each amb and interamb.

This appears to be the first record of the genus *Brochopleurus* from the Southern Hemisphere, Egypt and India being the two areas where it has hitherto been recognized—in both cases from strata regarded as Miocene. A very similar species occurs in the Waitakian stage (Middle Oligocene) of New Zealand, but further study will be required to determine if it is identical with the species from Australia.

As the genus *Brochopleurus* will be dealt with at greater length with other Tertiary Temnopleuridae in a later publication, no more need be given here than the brief diagnosis and a figure.

BROCHOPLEURUS Fourtau, 1920

Small forms of hemispherical shape. Pore-pairs in a nearly straight line. Primary tubercles non-crenulate, imperforate; a distinct radiating sculpture round the primary and partly also the secondary tubercles. Apical system (known in *B. sadeki* Fourtau) regularly dicyclic; gill-slits small, indistinct. Spines unknown. (Mortensen, 1943.)

Remarks

Brochopleurus australiae may be distinguished immediately from other species of the genus by the transverse sculpturing of the ambulacral mid-zone, which is absent in the Egyptian and Indian species. On the other hand, it is very closely related to the forms from the New Zealand Oligocene already mentioned, which share this feature.

A second specimen, No. 4688 of the National Museum of Victoria, from the same locality, is evidently referable to this species. Its dimensions are: height 4·5 mm., horizontal diameter 9·5 mm., peristome diameter, 3·3 mm.

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Probable Direct Development in Some New Zealand Ophiuroids.

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Probable Direct Development in Some New Zealand Ophiuroids.

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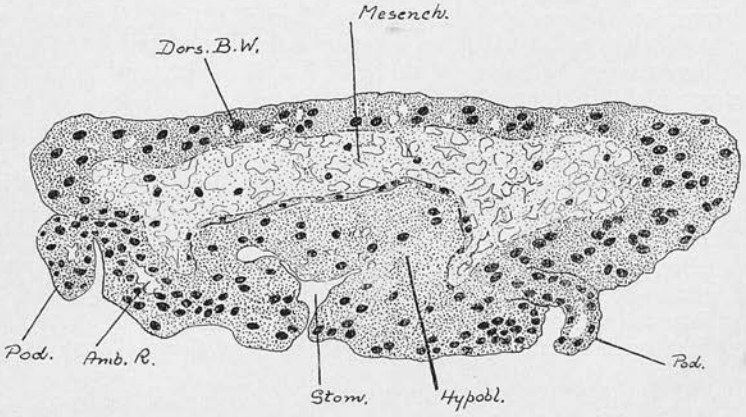
(Communicated by PROFESSOR H. B. KIRK.)

[*Read before Wellington Branch, October 23, 1940; received by the Editor, October 30, 1940; issued separately, June, 1941.*]

Ophiomyxa brevirima is a viviparous Ophiuroid occurring fairly commonly in the littoral zone of the New Zealand coast. Shortly before leaving New Zealand last year I obtained three adult specimens, two of them males and the third a female. The latter proved on examination to be carrying in the bursae some fifty young Ophiuroids, all at the same stage of development, or approximately so. The young, measuring about 0·7 mm. across the disc, were at that stage at which the outline of the body resembles in general form that of the starfish *Asterina*, having the arms as yet unsegmented. The opaque, buff colour of these indicates that the egg must be very yolky, so much so that the yolk still colours the greater part of the tissues in the "Asterina" stage. This conclusion is borne out by microscopic examination of sections of these stages, which indicates the presence of large numbers of yolk granules thickly distributed throughout, and staining with basiphilic dyes, but not masking the nuclei.

Vertical sections show that the coelom is represented by a remarkably extensive and clearly marked zone of typical mesenchyme. The cells are loosely aggregated, with protoplasmic extensions enclosing spaces. No coelomic cavity can be distinguished. From the evidence already provided by *Amphiura squamata* and by Kirk's Ophiuroid (referred to below) it seems fairly certain that this species



Vertical section through embryo of *Ophiomyxa brevirima*, showing mesenchyme mass occupying the position of the future coelom.

Dors. B.W., dorsal body-wall; Mesench., mesenchyme; Pod., podium; Hypobl., hypoblast; Stom., stomach; Amb. R., ambulacial ring.

must have a direct, or partially direct development. In all probability the coelom will be found to arise as splits in the mesenchyme mass referred to above, and shown in the accompanying figure. In the type of Ophiuroid development having a larval stage (hitherto regarded as the usual type of development for the group) the coelom is clearly differentiated from enteric pouches long before the radial form is assumed. *Ophiomyxa brevirima* should provide interesting material for research where sufficient specimens can be obtained.

In a preliminary paper in the *Transactions of the New Zealand Institute*, Professor H. B. Kirk (1916) recorded his discovery of the eggs of an Ophiuroid having a very abbreviated development. Subsequent work has shown that the egg, which is heavily yolked, divides to form a blastula with only a small and excentric blastocoel. Invagination is largely replaced by epiboly and the archenteron is only a transient feature, giving rise to no lasting structures. There is no larval stage, nor any vestige thereof. The coelom arises late in development as a series of splits in a mass of mesenchyme, and the stomach by a hollowing out of a mass of hypoblast. A young Ophiuroid at the " disc " stage leaves the egg. A general account of the development of this species is at present in the press, and will be published in England (Fell, 1940). None of the young of this species has as yet been reared to a stage sufficiently advanced for identification, nor have the parents of the eggs been discovered. Hence we are unable to refer to this interesting species by any scientific name. The writer till recently has been engaged upon research on the influence of yolk and viviparity on development in Ophiuroids, and the preliminary results to hand indicate that the type of development occurring in this New Zealand form is likely to prove by no means unique. It will therefore be necessary to have some convenient term by which this species may be referred to, since it is a " type " for this kind of development. There is as yet no justification for giving a new scientific name to the species on the assumption that it is a new form. On the other hand, it has been shown that the eggs cannot belong to any of the species commonly occurring in the area where they are found (Island Bay). Therefore, until the problem of their identity is finally cleared up, I suggest that the species be referred to as " Kirk's Ophiuroid," after the discoverer of the unusual type of development that it has.

Pectinura cylindrica and *P. gracilis* have both been shown to be viviparous and hermaphrodite, a condition closely approaching that found in *Amphiura squamata*. As the latter species has a partially direct development, we may expect that the two New Zealand species of *Pectinura* mentioned will be found to have a modified development also. *Pectinura maculata* is a larger form which is neither viviparous nor hermaphrodite. The eggs, however, are very heavily yolked, and therefore we can expect a modified development in this species, too. Here is abundant material for research by New Zealand workers.

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The Origin and Migrations of Australasian Echinoderm Faunas Since the Mesozoic

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Abstract

Similarities in the Tertiary echinoderm faunas of New Zealand and Australia are such as to indicate a common origin from the northern Indo-Pacific. Southward migration probably has occurred along the Indo-Malayan archipelago, or its Tertiary equivalents; but northward movements of Australasian genera into the Indo-Pacific can be detected from the Miocene onward. In the late Tertiary a west to east trans-Tasman faunal migration can be detected. Such similarities as exist between the echinoderm faunas of New Zealand and South America are probably a result of faunal contributions from the former to the latter. Possible mechanisms enabling faunal migration of echinoderms are considered.

The aim of this paper is to examine the general character and the generic content of the echinoderm faunas of Australia and New Zealand since the close of the Mesozoic; and also to offer a tentative interpretation of the data so far as they bear upon the problem of the origins of the faunas, and their migration routes into, out of, and within the Australasian region. Finlay's trans-Tasman correlations of 1947 are employed. The New Zealand palaeontological evidence is mainly based on unpublished studies still in progress. I am indebted to Dr. J. Marwick, to the late Dr. J. M. Finlay and to Dr. C. A. Fleming, all of the Geological Survey of New Zealand, for age determinations of the New Zealand material. The Australian records are taken mainly from the literature, and as far as possible their age-determinations have been revised in accordance with Finlay's views. In this I have had the assistance of Dr. J. Marwick. The generic placing of some of the material from Australia differs from that assigned to it in the older literature, and is more in accord with current ideas. The reasons for the changes will be given in a later publication. I am indebted to the Director of the National Museum of Victoria for the opportunity to examine fossils, and to others who have sent Australian specimens.

1. The Generic Content of the Tertiary Echinoderm Faunas of Australasia

(a) Early Tertiary.

Our knowledge of the Australasian echinoid faunas of the Cretaceous and Eocene is very fragmentary. In New Zealand occurred the Cretaceous *Micraster*,

and the Senonian starfish *Ophryaster* is represented by a species which closely recalls those of the Danish and English Senonian. From Western Australia a Cretaceous cidarid is known, but its generic position is uncertain.

During the Eocene the holasterid echinoid *Cardiaster* was present in both Australia and New Zealand, though it had by then already become extinct at the close of the Cretaceous in all other areas, so far as we know. *Nucleopygus* (syn. *Nucleolites*), another Mesozoic genus, was established in Australasia; we know it with certainty from Australia, and it may well yet turn up in the New Zealand Eocene. Elsewhere it was in process of extinction. Its lineage was destined to follow a long history in Australia and New Zealand, with Recent representatives in both areas (*Apatopygus*). In Australian Eocene sediments are also found *Salenidia* and *Prenaster*. In New Zealand are found *Schizaster, Galeraster,* Loveniidae of undetermined generic position (probably representing an undescribed genus), and some Echinometrid, possibly *Heliocidaris*. *Brochopleurus*, listed as an Oligocene immigrant below, has also been found in the Upper Eocene (Kaiatan) since this paper was set in type.

(b) Mid Tertiary.

Mesozoic holasterids continued to survive in New Zealand at the opening of the Oligocene, with *Cardiaster* and also *Echinocorys*, the latter genus not yet known earlier in New Zealand sediments. The two genera, however, do not seem to have survived into the mid-Oligocene. Another, and later, development of the holasterid stock is seen in *Duncaniaster*, which appears in the mid-Oligocene, and enters upon a prolonged history in the Australasian region.

Genera which first appear in the lower or middle Oligocene of New Zealand include a number of forms of large size. The assemblage includes the following, together with a few others not yet determined:—*Histocidaris, Phyllacanthus, Stereocidaris, Goniocidaris, Eucidaris, Prionocidaris, Grammechinus, Brochopleurus* (see Eocene), *Echinocorys, Duncaniaster, Fibularia, Studeria, Echinolampas, Planilampas, Maretia, Lovenia, Pericosmus, Linthia, Brissopsis, Cyclaster, Eupatagus, Brissus.* Also till such time as *Nucleopygus* is known with certainty from the New Zealand Eocene, it must be included here.

Contemporary Australian lower and middle Oligocene beds of marine origin are believed to be unrepresented stratigraphically. They may well have carried a similar faunal assemblage to those of New Zealand, since we find much the same kind of fauna in the Janjukian, which Finlay (1947) attributes to upper Oligocene plus lower Miocene. The Janjukian yields the following genera:—*Phyllacanthus, Stereocidaris, Goniocidaris, Eucidaris* (to which the unnamed club-shaped spines of Chapman and Cudmore (1934) must certainly be ascribed), *Prionocidaris, Paradoxechinus, Brochopleurus, Duncaniaster, Fibularia, Studeria, Echinolampas, Plesiolampas, Australanthus, Cassidulus, Echinoneus, Maretia, Lovenia, Pericosmus, Linthia, Schizaster, Brissopsis, Cyclaster, Eupatagus, Scutellina, Sismondia, Conoclypus, Monostichia, Coelopleurus, Gualtieria* and *Hemiaster;* as well as *Nucleopygus* which was earlier present.

New Zealand Miocene marine sediments are mainly of a non-calcareous and sandy facies, yielding little direct information on the echinoid faunas. We do know that *Schizaster* and *Pericosmus* persisted, the latter at least into the lower Miocene, the former till near the close of the period. It would seem probable that, where the environment was suitable, the Oligocene genera would have per-

sisted—in other words, the fauna would have resembled that known from the Australian Janjukian.

It will be seen that the two portions of the mid-Tertiary represented in Australia and New Zealand by echinoderm-bearing beds contain a similar assemblage of genera. The similarities, indeed, extend to the specific level, as in the case of *Brochopleurus*, which has similar or identical species on either side of the Tasman (Fell, 1949a), and *Duncaniaster* (unpublished evidence).

(c) Late Tertiary.

Profound changes in the Australasian echinoid faunas towards the close of the Miocene parallel those observed in the mollusca and other groups. These latter have been attributed to a cooling climate (Fleming, 1949), and the same conclusion might be drawn from the echinoid evidence. Thus, the disappearance of *Schizaster*, a supposedly warm-water genus, takes place in New Zealand at the close of the Tongaporutuan stage (Upper Miocene). The warm-water genus *Phyllacanthus* last occurs in New Zealand in the Kapitean stage (Uppermost Miocene).

Genera which disappeared from south-eastern Australia include *Duncaniaster, Lovenia, Linthia, Hemiaster, Gualtieria, Coelopleurus, Brochopleurus, Paradoxechinus, Monostichia, Sismondia, Scutellina, Nucleopygus, Cassidulus, Australanthus, Studeria, Plesiolampas,* and *Echinolampas.*

The New Zealand pre-Pliocene extinctions removed the following genera from the fauna:—*Schizaster, Duncaniaster, Lovenia, Linthia, Brochopleurus, Studeria, Planilampas, Echinolampas, Grammechinus, Fibularia, Maretia, Pericosmus, Eupatagus,* and all the cidarids, except apparently *Stereocidaris,* and perhaps *Goniocidaris.*

The following Miocene genera of Australia are still represented in the Recent East Australian Fauna, though not known from the Pliocene; they may have survived in warmer waters of the northern or north-eastern coasts:—*Prionocidaris, Eucidaris, Fibularia, Echinoneus, Maretia, Lovenia, Pericosmus, Schizaster, Brissopsis, Eupatagus;* and also the *Nucleopygus-Apatopygus* lineage, known from the Recent of Western Australia.

These losses were partly balanced by an accretion of new genera of modern aspect. *Clypeaster, Arachnoides, Peronella* and probably also *Pseudechinus* appeared in the Australian Lower Pliocene, whilst in the corresponding sediments of New Zealand (Waitotaran and Nukumaruan) we first meet with *Arachnoides, Pseudechinus, Echinocardium* and *Evechinus.*

The Recent echinoderm faunas of the two regions need not be summarized here; see, for Australia, Clark (1946), and for New Zealand, Fell (1949b).

2. The Origins of the Australasian Tertiary Echinoid Faunas

In seeking the origins of the faunas we need to compare the foregoing data with the known geological and geographical ranges of the genera concerned. The comparison may be simplified by treating the genera common to New Zealand and Australia as one group, and those not shared in common as two subsidiary groups.

(a) Tertiary Genera Common to Australia and New Zealand.

Cardiaster and *Nucleopygus* entered Australasia in the Eocene. They had previously been abundant in the northern old world in the Cretaceous. Of the

genera which entered Australasia during the early and mid-Oligocene, *Phyllacanthus* and *Cyclaster* had already become established in northern India in the Eocene. *Fibularia, Studeria, Pericosmus* and *Lovenia* likewise occur in the Eocene of Egypt, though they do not occur in Australasia till the Oligocene. *Echinolampas,* another Oligocene immigrant to Australasia, had had a wide northern distribution in the Eocene, in India, Borneo, North Africa, and Europe. *Pericosmus* had also occurred in the Eocene of Persia, and reached India by the Oligocene at least, probably earlier. *Linthia, Schizaster* and *Brissopsis* had all had a widespread northern distribution during Cretaceous and Eocene times. The remaining Oligocene genera, *Duncaniaster, Goniocidaris* and *Brochopleurus* are not known earlier in the geological record; they probably originated within the Australasian region, and will be further considered below. Of late Tertiary and Recent immigrants to Australasia, *Centrostephanus* and *Echinocardium* had already appeared in Europe in the Miocene, *Brissus* in the Miocene of Java, *Laganum* in the Eocene of the Mediterranean. *Holopneustes* and *Pseudechinus* are perhaps Australasian derivatives of the Temnopleurid stock previously present in the Miocene. *Clypeaster* is probably an immigrant from the north-west Pacific. from an original Pliocene Californian stock. *Arachnoides* and *Monostichia* are Australasian.

(b) Tertiary Genera of New Zealand, Not Yet Known From Australia.

Galeraster and *Echinocorys,* in the New Zealand Eocene and Oligocene, are the last remnants of ancient northern stock. *Grammechinus,* in the lower Oligocene, seems to have been the first of its type—it reappears in the Miocene of India, and is known only from these two records. The genera *Evechinus* and *Ogmocidaris* are both restricted to the New Zealand submarine plateau, the former first appearing in the mid-Pliocene.

(c) Tertiary Genera of Australia, Not Yet Known from New Zealand.

Echinoneus, Sismondia, Conoclypus, Cassidulus, Prenaster and *Plesiolampas* all had Eocene representatives in India or Europe; they are not known from Australia earlier than the Janjukian, save for *Prenaster,* which occurs in an Aldingan (lower) sediment, attributed to the late Eocene. *Coelopleurus* occurred throughout the Oligocene in India; it is present in the Australian Janjukian.

Indo-Pacific Origin.

From the foregoing we may conclude that the main source of the Australasian Tertiary echinoderm faunas has been the old world, and more particularly, the northern Indo-Pacific region. Genera which occur in India in the Cretaceous reached Australasia in the Eocene. Genera which occur in the Indian Eocene reached New Zealand by the early or mid-Oligocene; they may well have reached Australia at the same time, but the absence of earlier Oligocene beds from Australia precludes our recognizing these forms earlier than the Janjukian. This Old Indo-Pacific stock, as it might be termed, seems to have remained with but little change until the close of the Miocene. Then, with extinction of the old fauna, came a New Indo-Pacific stock, which, together with stock of Australasian origin, brought into being the late Tertiary and Recent faunas. We find the earliest members of this new stock in the Waitotaran and Nukumaruan stages of the New Zealand early and mid-Pliocene and in the Kalimnan (early Pliocene) of Australia.

Genera of Australasian Origin.

It would seem that the genera *Brochopleurus, Goniocidaris, Gramechinus* and *Duncaniaster* originated in or near Australasia during early or mid-Oligocene times. All except *Duncaniaster* had reached India by the Miocene, and *Brochopleurus* also spread to Egypt during the latter period. The Indian species of *Brochopleurus* resemble the Egyptian, and both differ in the same way from the Australasian forms, (especially as regards the specialized transverse epistroma of the ambulacra). The Australasian lineage includes extremely similar forms in the Waitakian-Duntroonian of New Zealand (lower to mid-Oligocene) on the one hand, and in the Janjukian of Australia on the other. *Goniocidaris* has left a trace of its northern passage in a Miocene Indonesian species. The main development of the genus occurred during the Tertiary in Australasia, and it is still well represented in the latter region at the present time, though there is also a Recent distribution arc running northwards through Indonesia and Malaya as far as Japan. *Duncaniaster,* which is restricted to Australia and New Zealand, ranges from mid-Oligocene to mid-Miocene (Balcombian of Australia).

Arachnoides, a sand-dollar, is a genus of Australasian origin which arose at the end of the Miocene, apparently as a development of the *Monostichia* stock then present in Australasia. *Monostichia* itself, likewise an Australasian stock, is of unknown derivation. The main development of the *Arachnoides* group of species has been in Australia, with one early Pliocene species, and three Recent. It had already entered New Zealand by the early Pliocene (Waitotaran stage), and there is one Recent species. *Arachnoides* also spread northward into Java during the Pliocene, and apparently its northern extension has been proceeding actively since that time. Its north-western limit in Recent faunas is located at the Andaman Islands, whilst Samoa marks its north-eastern boundary. It has not spread elsewhere, and is absent from the sub-Antarctic portion of the New Zealand plateau.

3. Tertiary Migration Routes to Australasia

A Tertiary archipelago like the existing Indonesian-Malayan arc, with its associated marginal shallows, and relatively narrow deeper-water gaps, would provide an adequate migration path for all the faunal movements inferred above. The movement of lineages must have been mainly southward but, as indicated, appreciable traces of northern migration out of Australasia seem discernible. This northward efflux seems to have occurred from the Miocene period onwards.

Southward migration has probably been fairly continuous since Eocene times. It appears that New Zealand had a relatively direct link with the Indo-Pacific during the greater part of the Tertiary. South-eastern Australia must have had a similar connection in the Eocene, and from Janjukian times onwards—perhaps also in the Oligocene, for which we lack evidence at present. So far as faunal movements are concerned, these links can be treated as one, and they may well have been mainly one and the same in fact. Just as we are justified in using the term "Australasian" to describe the echinoderm faunas (instead of distinguishing the two component portions), so also it would be justifiable to speak of an "Australasian" shallow-water link with the Indo-Pacific. It is desirable to make this point, since recently H. L. Clark (1946), without recourse to the fossil record, has maintained an entirely different derivation for the New Zealand echinoderm fauna from that of the Australian; his views are further considered in the next section of the present paper.

The Australasian shallow-water route to and from the northern Indo-Pacific may well have been interrupted by partial barriers, such as land, or deep-water gaps, during early and mid-Tertiary times, because it would seem that it could not be traversed rapidly in either direction by shallow-water, bottom-dwelling forms. Genera moving either northwards or southwards appear at the opposite extremity of the arc several geological stages later than the date of their first appearance in the geological record.

4. Migration Between New Zealand and South America

If there are any South American or Falkland elements in the Tertiary echinoderm faunas of Australasia, they cannot as yet be recognised. Characteristic central and southern American Tertiary genera such as *Oligopygus,* and the family Scutellidae, have no Tertiary or Recent representatives in either New Zealand or Australia. Genera which spread from the old world down through the Americas, such as *Micropsis, Psammechinus, Lutetiaster* and *Agassizea,* have not reached Australasia at any stage, so far as we know. The Antarctic genus *Abatus* is absent. Characteristic genera of Australia and New Zealand are not shared with South America, or at most, have a single Tertiary representative* in South America. The genera which are common to Australasia and to South America are likewise shared with the old world. There are more genera shared with the old world than with South America.

However, a small but perhaps significant South American relationship can be detected in the Recent echinoderm fauna of New Zealand. It is most marked in the southern half of the New Zealand plateau, especially in the sub-Antarctic Islands which stand on the Campbell Plateau, or on the somewhat deeper eastern extension of that plateau. Here are found four genera which have South American representatives, and three of them are without representation in Australia; there are, in addition, a few species of cosmopolitan genera (*Amphiura magellanica, Cucumaria calcarea, Gorgonocephalus chilensis*) which are shared by South America and New Zealand.

H. L. Clark (1946), apparently impressed by these facts (though he does not specify the grounds for his opinion in other than general terms), contended that the New Zealand Recent echinoderm fauna is of southern origin, whereas that of Australia he holds to be of Indo-Pacific derivation. His views were based only on Recent faunas. The presence of some Australian echinoderms in New Zealand was explained by Clark as resulting from the trans-Tasman drift of dead tests, in sea-weed. Proof that living specimens of these species do in fact inhabit northern New Zealand has since been furnished (Fell, 1949c). Mortensen (1925, 1951) strongly opposes the views of Clark. He deduces, again on the basis of Recent faunas, a common Indo-Pacific derivation for the echinoderm faunas of both New Zealand and Australia. His conclusions are concordant with the fossil record as analysed in this paper.

What, then, is the significance of the element in the Recent New Zealand echinoderm fauna which suggests some South American connection? The following interpretation is offered as an attempt to reconcile the Tertiary and Recent evidence. New data on the Recent sub-Antarctic faunas have become available

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* Namely, the problematic "*Echinus*" *andinus* Philippi.

as a result of the New Zealand Cape Expedition of 1941-45, and subsequent expeditions; these have added to our knowledge of the echinoderms of the Snares, Auckland Islands, Campbell Island and Antipodes Island (Fell, 1953). Supplementary data are also supplied by the collections at Macquarie Island and Heard Island, material which is now coming to hand, from the Australian Antarctic Research Expedition.

First, *Amphiura magellanica*, like the other species mentioned with it above, is to be regarded as circumpolar. It was collected on two occasions from *Macrocystis* holdfasts by W. H. Dawbin at the Auckland Islands. The tougher portions of the large southern brown algae can drift for long distances in the circumpolar west to east currents, or before the west wind drift. A recent observation of drifted *Durvillea* in Australian waters is relevant (Moore and Cribb, 1952); the nearest known source to the west is Kerguelen Island, 5,000 miles distant.

Secondly, we have to account for the presence in New Zealand and South America of representatives of the genera *Pseudechinus, Calvasterias, Asterodon* and *Stichaster*.

The majority of the Recent species of *Pseudechinus* are Australasian, and about half of the total number are restricted to New Zealand. The remainder are scattered around the sub-Antarctic Islands, with no more than a single species (usually endemic) at each point; one of these, *P. magellanicus* occurs in Patagonia. The genus has been well represented in Australasia at least since mid-Pliocene times. A supposed South American Miocene species is inadmissible on present evidence, and certainly cannot be used as proof of the earlier origin of the genus in South America. On the other hand, all the evidence points to Australasia as the original (and present) home of the genus. The other species are therefore odd derivatives, or "escapes" from the Australasian parent stock.

All the New Zealand species of *Calvasterias, Asterodon* and *Stichaster* are endemic; some are restricted to the sub-Antarctic Islands standing on the Campbell Plateau, which runs south from New Zealand. Like *Pseudechinus, Asterodon* is more highly speciated in New Zealand than in South America. There is one New Zealand species of this genus which is so distinctive that it has been considered as a distinct genus (*Diplodontias*) by earlier workers. These facts suggest that *Asterodon* can hardly have been a recent immigrant to the New Zealand area (where its species do not exhibit mere geographic speciation to any marked extent)—but *Asterodon* might well have been a relatively late immigrant to South America. The endemism exhibited by *Calvasterias* and *Stichaster* likewise argues against a recent derivation from South America. Further, it might be noted that each genus includes in New Zealand at least one eurytopic species. This feature, as has been pointed out elsewhere (Fell, 1949b) characterizes some of the most typical of New Zealand echinoderms; forms like *Evechinus* for example, so morphologically separated from exotic types, are widely ranging within the New Zealand area, though absent elsewhere—so that morphology and distribution both point to a relatively early differentiation within the New Zealand area. We can conclude that New Zealand is probably the older home of these genera, whilst South America is more likely to have been a later recipient of occasional offshoots from the New Zealand stock. Mortensen (1925) recorded an observation of drifting algae carrying *Calvasterias* during his visit to the Auckland and Campbell Islands. Epiplanktonic material

of this type might well drift before the west to east circumpolar currents, or the west wind drift, to reach the Magellanic area, or even to be carried north on the Humboldt Current to the coasts of southern Peru. Climatic factors would prevent any great spread to the warmer waters (of the surface) to the north.

The whole echinoderm fauna of the New Zealand sub-Antarctic Islands has a close affinity with that of the mainland area. It can hardly be doubted that this southern New Zealand fauna shares a common origin with that of New Zealand proper, and that it reached its present situation by way of the New Zealand submarine plateau. It is unlikely that it came from South America; it is quite likely that it supplied contributions to the southern South American fauna.

5. Trans-Tasman Migration

The earlier and mid-Tertiary successions on either side of the Tasman Sea are insufficiently complete to make any deductions as to faunal migrations within Australasia. Certain features of the echinoid time-ranges have suggested to me that possibly the Janjukian includes a middle Oligocene horizon; but the evidence of forams and molluscs apparently does not support this view. The presence of the large fossil penguin *Palaeeudyptes* in supposed Miocene sediments of Australia does, however, invite comparison with the lower Oligocene (Duntroonian) of New Zealand (a point to which Dr. C. A. Fleming kindly drew my attention). At all events, the echinoid succession on either side of the Tasman is not yet adequately correlated in regard to finer details at or near the specific level. The evidence from the late Tertiary is clearer and, I think, susceptible to inductive treatment.

Pliocene and Post-Pliocene trans-Tasman echinoderm migrations have occurred, and they have been essentially from east to west. So far as Recent species are concerned, the movement has been, more precisely stated, from eastern Australia towards northern New Zealand, particularly to that northern extension of the North Island coastline now usually referred to by Finlay's term Aupourian. Common Australian Recent echinoids, for example *Centrostephanus rodgersii, Holopneustes inflatus* and *Heliocidaris tuberculata,* occur in small numbers at various points in North Auckland, notably at Cavalli Island. *Phyllacanthus parvispinus* occurs at the Kermadec Islands. On the other hand, correspondingly common New Zealand echinoids are completely unknown from any Australian fauna. *Evechinus,* for example, the commonest and most widespread New Zealand echinoid, would seem to be admirably equipped to take advantage of any reverse east to west dispersal mechanism if it existed. It is eurytopic (ranging through eighteen degrees of latitude), it has a large pelagic larva, it has already succeeded in traversing the deep water gap between New Zealand and the Kermadec Islands, and it has been present in New Zealand at least since the lower Nukumaruan (early middle Pliocene). Yet it is known only from the New Zealand region.

Another argument in favour of deducing that any trans-Tasman migration must have been from west to east, and not the reverse, is provided by the high proportion of endemic Recent species of New Zealand echinoderms (some 80 per cent. of species). It is recognised that this is indicative of Tertiary isolation, especially of late Tertiary and Recent isolation. But the isolation implied is rather that of an outpost with a one-way traffic highway, along which new im-

migrants can occasionally travel from without, and along which few forms can return.

Before considering the probable generic content of the faunas which must have crossed the Tasman at successive stages since the Miocene, we may pause to discuss briefly the relative importance for echinoderm dispersal of ocean currents on the one hand, and former shallow ridges (such as the New Zealand Ridge, or Lord Howe Rise) on the other.

The East Australian current flows southward along the eastern coast of Australia to about latitude 40 degrees south, where it encounters the west wind drift. The junction results in a counter-clockwise swirl, which strikes towards New Zealand. According to Sverdrup, Johnson and Fleming (1942) the February surface isotherms along the 40 degrees parallel in the Tasman form east-west zones of water, the temperature of which is around 18 degrees Centigrade. Mortensen (1921) has provided some minimum figures for the life-span of the pelagic stage in some New Zealand and Australian echinoderms, from which it appears that a free-swimming larval stage of five or six weeks may well be common (for example, *Evechinus* larvae showed no sign of metamorphosis over the developmental period from December 18 to January 22; the pelagic stage of *Heliocidaris tuberculata* is over five weeks); the total pelagic life-span may well be longer. However, comparative embryology would lead one to deduce that the total pelagic life is not likely to exceed appreciably a tally of about eight weeks. On the evidence of Fleming (1952), this seems scarcely sufficient to enable a trans-Tasman crossing on the existing East Australian current of between four and a-half and nine miles per day (unless the pelagic stage were succeeded by an epiplanktonic phase on drifting algae, such as does occur in some starfish and ophiuroids). However, Fleming (1952) points out that it is possible that parts of the East Australian current may flow at speeds up to 30 miles per day, so that we cannot yet dismiss the possibility that genera like *Heliocidaris* may make the trans-Tasman crossing in the larval stage. *Astropecten,* with a larval period of a little over three weeks, could not; yet *Astropecten polyacanthus* seems undoubtedly to be a relatively recent immigrant to New Zealand from the Australian-Indo-Pacific area.

One cannot dismiss the possibility of migration along the present shallow-water ridge through the Lord Howe Rise during late Tertiary and Pleistocene lowerings of sea-level. In this connection the evidence from the sub-Antarctic is apposite. The present echinoderms faunas of Auckland and Campbell Islands have clearly been derived from New Zealand. These islands are linked with the New Zealand mainland by the shallow Campbell Plateau (Fleming and Brodie, 1951), which is nowhere deeper than 500 fathoms. Macquarie Island, in the same area, is separated from them by deep water of over 2,000 fathoms. Its echinoderm fauna is almost entirely Antarctic in character, and clearly has not been derived from New Zealand, though a single echinoid (*Pseudechinus novaezelandiae*) is shared; the latter has a pelagic development. This evidence seems to imply that a shallow route is more effective for echinoderm dispersal than is a much narrower, but deeper, gap—unless the gap is traversed by a favourable current. Thus, so far as the Tasman is concerned, I am inclined to attach some importance to the Lord Howe Rise as at least a former, if not a present, dispersal route.

Considering now the generic content of the faunas concerned in trans-Tasman immigration:—*Arachnoides*, as already noted, had entered New Zealand by early Pliocene (Waitotaran) times, and no doubt came from eastern Australia. A mid-Pliocene New Zealand species much resembles a species still found in Recent Queensland waters. The Recent New Zealand species is distinct, but it too occurs in east Queensland seas. It may well be a second, later immigrant to New Zealand. *Peronella*, an Indo-Pacific genus, had reached Australia by the Pliocene, and it may well have spread to New Zealand at about the same time, for the one Recent New Zealand species is endemic. Australia has five Recent species, three of them endemic. Perhaps *Ctenamphiura* was a Pliocene immigrant —the genus is confined to north-east Australia and New Zealand, with an endemic species at either extremity of its range; its fossil history is unknown.

Of genera which probably crossed the Tasman Sea later on, in Pleistocene or Recent times, the following may be noted as having one (or more) identical Recent representatives on both the New Zealand and east Australian coasts:—*Araeosoma, Holopneustes, Heliocidaris, Clypeaster, Laganum, Stichopus, Lipotrapeza, Mensamaria, Chiridota, Asterodiscus, Astrobrachion, Ophiocreas, Ophiactis;* and perhaps a second instalment of *Arachnoides*.

Some Indo-Pacific forms also arrived at a late date, perhaps by way of the Lord Howe Rise—for example, *Brissopsis, Brissus, Astropecten* and *Coscinasterias* all have identical, or very similar species both within and beyond New Zealand waters.

Apatopygus and *Goniocidaris* probably owe their present distribution on either side of the Tasman, not to any trans-Tasman migration of the type that has been considered above, but to the fact that their Recent species are a heritage from the former mid-Tertiary common fauna of Australasia. The ancestors of these forms may have arrived along shallow-water routes no longer existing. They represent an archaic element shared by Australia and New Zealand. *Apatopygus* has one abundant, endemic species in New Zealand, and one rare southern Australian species. The differences between the New Zealand and the Australian species seem at least as great as those between either of them and their Tertiary ancestors in the *Nucleopygus* lineage. The lineage is a conservative one, showing but little change over its long history; and the name *Apatopygus*, which is applied to the two Recent species, does not really cover any generic difference from the fossil genus—as Mortensen has shown (1948).

Summary

(1) The Australian and New Zealand Tertiary echinoderm faunas show marked similarities throughout those portions of the stratigraphical record represented by comparable deposits on either side of the Tasman Sea. They stem from a common origin in the northern Indo-Pacific.

(2) The Indo-Malayan archipelago, or its Tertiary equivalents, could well have provided the shallow-water migration route, both into Australasia and from Australasia. The route may never have been a very easy one for echinoderms to traverse, as considerable time-delays seem to elapse between the first occurrence of a genus at one end of the arc, and its first appearance at the opposite extremity.

(3) Migration of genera has been mainly southward. Nevertheless, northward movement of genera believed to have originated in Australasia, can be detected from the Miocene onward.

(4) Trans-Tasman faunal migration is not, on present evidence, determinable for the early and mid-Tertiary faunas, but in the late Tertiary and Recent it has been from west to east—that is, from Australia to New Zealand.

(5) A small archaic element common to the Recent faunas of Australia and New Zealand stems from a common mid-Tertiary fauna, and does not indicate later trans-Tasman movement.

(5) Certain genera of New Zealand, or Australasian, origin have supplied contributions to the South American fauna, probably by means of the west to east circumpolar and west wind drifts. There is so far no evidence of South American elements in the Tertiary echinoderm faunas of Australasia.

(6) The Recent echinoderm faunas of the Auckland, Campbell, Snares and Antipodes Islands, in the sub-Antarctic, have drawn their component genera and species from the New Zealand mainland fauna. These islands have a relatively shallow-water connection with New Zealand. The Recent echinoderm fauna of the nearby Macquarie Island, which stands in deep water, has been derived from the Antarctic, with the exception of one New Zealand echinoid. The latter has a pelagic larva.

(7) It is concluded that shallow-water routes are of more importance in the dispersal of echinoderms than are relatively narrow deep-water gaps, unless the latter are traversed by a favourable ocean current. Trans-Tasman migration has probably made use of both former shallow-water routes and of planktonic dispersal of larvae in the East Australian current.

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With the Compliments of the Author

AN UPPER CRETACEOUS ASTEROID FROM NEW ZEALAND

By H. BARRACLOUGH FELL
Victoria University College,
Wellington, New Zealand

From Rec. Cant. Mus. Vol. VI No. 2
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CHRISTCHURCH NEW ZEALAND
15 August 1952

AN UPPER CRETACEOUS ASTEROID FROM NEW ZEALAND

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ABSTRACT

Ophryaster novaezelandiae sp. nov. is described from the upper Cretaceous (Senonian) strata of New Zealand. The genus is characteristic of Senonian sediments of northern Europe and has not hitherto been recorded from the southern hemisphere.

ASTEROIDS of the family Goniasteridae are represented in the recent fauna of New Zealand by the genera *Mediaster, Nectria* and *Pentagonaster.* As yet no representatives are known fossil from the New Zealand Tertiary, though it seems highly probable that they are present; perhaps their remains, as disarticulated fragments, have escaped the notice of collectors. It is therefore of great interest that well-preserved specimens of a species referable to the Goniasterid genus *Ophryaster* have been found in an upper Cretaceous horizon in North Canterbury. *Ophryaster* till now has not been recorded from the southern hemisphere, nor indeed from anywhere else save northern Europe, where it characterizes the upper Cretaceous of England, Denmark and Germany. The present record is also the first asteroid to be reported from the New Zealand Mesozoic.

ORDER *PHANEROZONIA*

FAMILY GONIASTERIDAE

Genus *OPHRYASTER* Spencer, 1913

Ophryaster novaezelandiae sp. nov.

Dimensions: Of medium size. Holotype – R, 50 mm.; r, 20 mm.; R/r, 2.5. Syntype – R, 43 mm.; r, 19 mm.; R/r, 2.26; maximum height (at interradial margin), 5 mm.

Disc stellate-pentagonal, the interradial margins concave, curving adradially to form the slender, tapering, acuminate arms. Abactinal area stellate-pentagonal, bounded by robust marginals and extending into the proximal half of each arm.

Superomarginal plates near the interradius are rectangular, about twice as broad as long; a typical plate measures 5 mm. by 2.5 mm., by 2 mm. height. Towards the mid-radius the superomarginals become squarish, about 3 mm. across, by 1.5 mm. in height. They remain quadrate or subquadrate for the remainder of the arm, decreasing in size towards the tip. Terminal ossicles are not preserved. The sculpture of the superomarginals is for the most part abraded on both the holotype and syntypes; in a few cases however, it can be distinguished faintly. On one, the seventh superomarginal from the interradius of one side, the sculpture is as in Figure 1. Numerous spine-pits are evenly scattered over the outer two-thirds of the

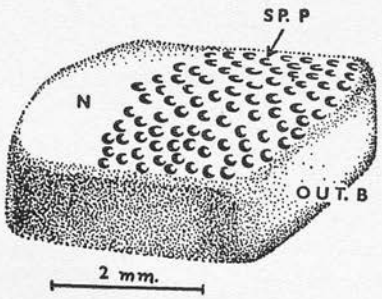

Fig. 1

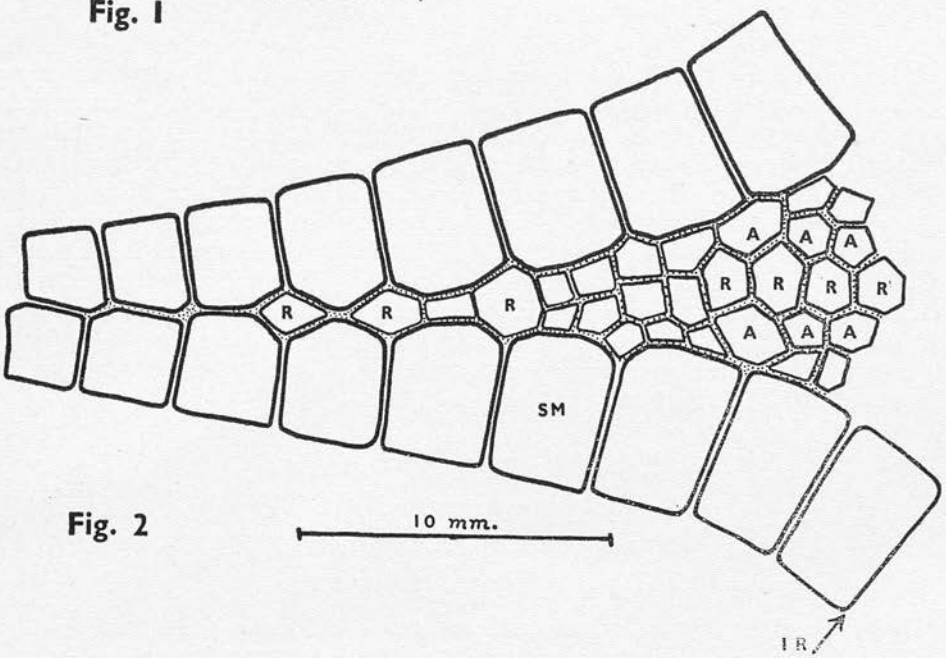

Fig. 2

FIG. 1 Superomarginal plate, the seventh outward from the interradius, showing sculpture. N, Naked inner zone of upper surface. OUT.B., Outer border. SP.P, Spine-pit.

FIG. 2 Proximal region of arm from above, partly restored. A, Adradial abactinal ossicles. IR, Interradius. R, Radial abactinal plates. SM, superomarginal.

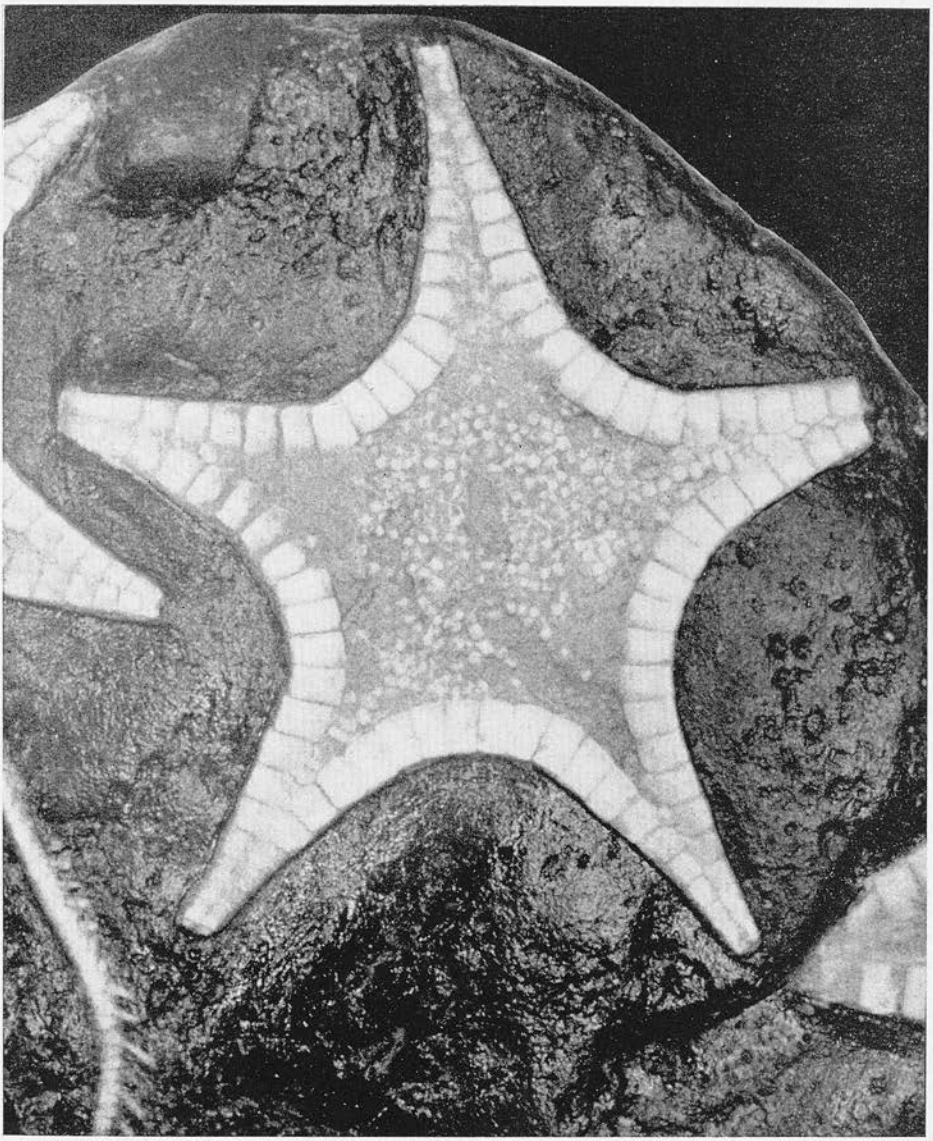

PLATE 1 *Ophryaster novaezelandiae,* holotype.

upper surface, leaving a proximal naked zone which borders the abactinal area. The spine-pits are all circular, each ca. 200 mu in diameter, separated one from another by ca. 100 mu on the average, occasionally touching one another. No spines remain. The sculpture of the outer surface is obscured in the specimens.

Inferomarginals apparently similar in number, arrangement, and shape to the corresponding superomarginal series, their sculpture obscured.

A complete interbrachial arc (arm-tip to arm-tip) comprises approximately thirty marginals. Along the distal half of the arm, beyond the outermost radial abactinal plate, the adjacent superomarginals are contiguous, but not exactly opposite their corresponding members, a tendency to alternation thus appearing (Figure 2).

The abactinal plates are markedly tabulate, flattened on their upper surfaces, polygonal, varying in size from about 1 mm. to 2 mm. across, forming a tessellated pavement, without papular spaces. No traces of paxillae occur, nor pedicellariae ; the latter, however, may have been present, but subsequently lost in preservation. There is a more or less distinct series of hexagonal radial plates along each radius in the inner part of the disc, but the series are interrupted distally, terminating in several isolated polygonal plates at the mid-radius of each arm, wedged between the marginals (Figure 2). The adradial plates are polygonal, not arranged in distinct longitudinal series, nor distinctly separable from the radial plates at the bases of the arms. The other abactinal plates are irregularly scattered in the holotype and syntypes owing to faulty preservation. The sculpture of the abactinal plates is nowhere evident.

Actinal surface and madreporite unknown.

Holotype and syntypes on a single slab now preserved in the Canterbury Museum. The holotype is the almost complete specimen illustrated in Plate 1.

Type Locality : The slab was found on the Cotswold Station, Omihi, in the bed of a tributary stream of the Motunau River, North Canterbury. It was brought to the Canterbury Museum by Mrs M. C. Little.

Horizon : Professor R. S. Allan of Canterbury University College, who kindly undertook the task of determining the geological horizon, writes as follows (private communication, June 4, 1951) : ' Some time ago B. W. Collins, M. Gage and I visited the area but failed to find additional specimens. I understand that our specimen was collected from a boulder in a creek. We saw the exact spot and it is almost certain that the slab is from the Uppermost Cretaceous (Senonian) strata of the district.'

Discussion : The general facies of the specimens recalls that of the recent *Nymphaster-Rosaster* group. The genus *Ophryaster* was erected by Spencer (1913) to accommodate certain European Cretaceous sea-stars which had originally been referred by Sladen to *Nymphaster,* but which differed from recent *Nymphaster* species in having the abactinal ossicles closely tessellated, leaving no room for papular pores. Other generic features of *Ophryaster* have recently been discussed by Rasmussen (1950) All of them agree well

with the present species, with the sole exception of the following detail of the superomarginals. In *Ophryaster* from Europe the superomarginals of the interradius present two oblique facets on the proximal border, one directed obliquely upwards towards the abactinal area, the other obliquely downwards towards the body cavity. Similar facets cannot be observed in the New Zealand material. In other respects the diagnosis of *Ophryaster* is so closely exhibited that, in my opinion, it would be absurd to separate the New Zealand material solely on the difference in regard to the facets. It is therefore referred to Spencer's genus, of which the genotype is *Ophryaster oligoplax* (Sladen).

As full accounts of the three European species of Ophryaster are not available in New Zealand, I am unable at present to suggest possible relationships between any of them and the New Zealand species ; sufficient information is available, however, to show that the latter is certainly distinct. *O. novaezelandiae* differs from *O.magnus* Spencer in the following respects: (1) Interradial marginals, which are broader than long in the former, longer than broad in the latter; (2) the arms of *O. novaezelandiae* taper more sharply ; (3) though the surface sculpture of the marginals is similar in the two species, the upper facet (or ' brow ', as Spencer, 1913, terms it) is by no means obvious in *O. novaezelandiae*—if, indeed, it is present at all.

The marginal plates do resemble those of *O. oligoplax* (Sladen) as regards their shape and sculpture, but again are distinguished by lacking the upper facet. From *O. lunatus* (S. Woodward) the new species differs by possessing the inner naked zones on the upper surface of the superomarginal plates—a structure which is absent from *O. lunatus* according to Spencer (1913).

It will be noted that the three European species are more closely related to one another than to the New Zealand one in respect to the possession of the inner facet. This suggests a parallel in the case of two earlier Mesozoic genera of echinoids. In *Dicyclocidaris* and *Miocidaris* it has previously been shown (Fell, 1950) a close relationship existed in the late Triassic between New Zealand and northern hemisphere forms. Both genera of cidarids are at the equivalent evolutionary stage, and might be considered congeneric were it not for the fact that the New Zealand form *Dicyclocidaris* has a double ring of scrobicular tubercles as against the single ring in *Miocidaris,* the northern genus. Thus it now begins to look as if we may expect to find other parallels between the Mesozoic echinoderms of Europe and New Zealand, despite the present lack of corresponding fossil records from intervening points on the globe. In other words, the isolation which seems to have invested the New Zealand fauna throughout the Tertiary seems not to have existed during the Mesozoic.

Ecology : The four specimens of *O. novaezelandiae* occur in the same bedding-plane, together with a crinoid fragment, on a slab of calcareous muddy matrix. The inference would seem to be that they were all overwhelmed suddenly *in situ* on a soft muddy sea-floor. The presence of the crinoid imples clear water conditions—which must have suffered a rapid mud invasion, with fatal result. The rare circumstance of finding four specimens

all with the ossicles associated in their natural positions also implies very rapid imbedding, for sea-stars disintegrate quickly after death.

Value as an index fossil : *O. novaezelandiae* possesses robust ossicles of characteristic form and sculpture. As in the case of the European Cretaceous, there is every reason to expect that such ossicles will commonly be found isolated in Senonian strata of suitable facies. They should be recognizable from the information here given.

ACKNOWLEDGMENTS

I have to thank Dr R. Duff, Director of Canterbury Museum, and Mr R. Forster for the opportunity of examining the type material ; Professor R. S. Allan for information on the age of the specimens ; and Mr A. Eady, of Victoria University College Zoology Department, who photographed the holotype for Plate 1.

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With the Author's Compliments.

A GIANT HEART-URCHIN.

BY

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A Giant Heart-urchin

Brissus gigas n. sp.

From NEW ZEALAND

By H. BARRACLOUGH FELL,

Victoria University College, Wellington.

The giant heart-urchin which is the subject of this paper was taken in deep water off the Bay of Islands and is now preserved in the collection of the Auckland Museum. It is evidently an undescribed species exceeding in size any echinoid hitherto known from New Zealand waters. As set out in the discussion below, there are grounds for believing that the specimen may ultimately become the type of a new genus, but in the meantime owing to the paucity of material it has been deemed advisable to place it in the genus *Brissus*, with which it most closely agrees.

The large size of the specimen has necessitated considerable reduction of the photographic figures. As the ornamentation and other surface features o fthe test are relatively unaccentuated, and consequently difficult to photograph, the location of the chief features shown on Plates 13 and 14 may be indicated here before proceeding to the diagnosis. On the abactinal aspect the peripetalous fasciole, which in life would carry a band of ciliary radioles, may be discerned following a zigzag course, enclosing the lateral and posterior pairs of petaloid ambulacra, curving sharply inwards in the intervening interambs, and tracing a broad convex sweep across the anterior part of the test. On the actinal side the large sternal plastron of the posterior interamb is delineated by its dark border, and occupies all the medial region posterior to the peristome. The sub-anal plastron, lying between the sternal plastron and the periproct, is foreshortened in this aspect, but the sub-anal fasciole by which it is circumscribed can be discerned. The latter structures are shown in full view in Text Figure 2, while Figure 1 gives details of the apical region.

Genus **BRISSUS** Leske, 1778.

Peripetalous fasciole present, but no internal nor anal fascioles; petals well formed and depressed; sub-anal fasciole complete, surrounding a distinct sub-anal plastron.

Brissus gigas n. sp. Plates 13 and 14; Text Figures 1 and 2.

Diagnosis: Test very large and inflated, without anterior notch, broadly ovate, truncate posteriorly. Apex and peristome markedly praecentral; the periproct situated on the obliquely truncate postero-ventral border of the test. Petals I, II, IV and V narrow and deeply sunken, as wide as deep. Ambulacrum III flush with test. Interambulacrum 5

keeled obliquely above, posterior to the peripetalous fasciole, and less markedly so below the sub-anal fasciole. Sternal plastron showing traces of radial fan-like furrowing and a radial arrangement of the fine tubercles on it. Primary tubercles extending within the peripetalous fasciole in interambulacra 2 and 3.

Length, 185 mm. Breadth at level of apex, 145 mm. Greatest breadth (at level of posterior extremities of petals I and V), 167 mm. Height from apex to labrum, 90 mm. Greatest height (from a point midway between apex and posterior ambitus), 100 mm.

Locality: Off Bay of Islands, North Auckland, New Zealand.

Depth: Not recorded; stated to be from "deep water." Fragments of what may be the same species have been taken at Pt. Abercrombie, Gt. Barrier Island, from an estimated depth of ca. 20 metres.

Holotype: In the Auckland Museum.

The specific name proposed refers to the large size of the spatangoid.

Fuller Account.

In view of the systematic problems raised by this specimen, a fuller account follows.

The material comprises a solitary denuded test, bleached to a pale creamy colour except within the peripetalous fasciole and in interambulacra 2 and 3, which are pale greyish. When collected the test was enveloped in a coralline alga, so that it is evident that the animal had been dead for some time. No trace could be found of any adhering radioles.

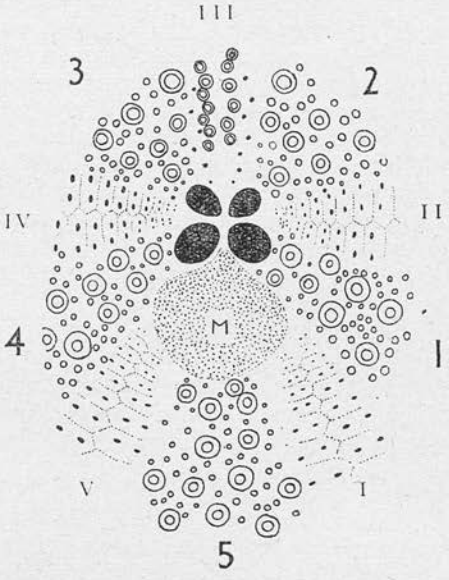

Fig. 1. Apical region. M., madrepore; I-V, Ambulacral columns; 1-5, Interambulacral columns, x 2.5.

The tuberculation extends over the whole of the interambulacral regions, but interambulacra 2 and 3 are distinguished both within and without the peripetalous fasciole by possessing larger primary tubercles. Only the primary tubercles are perforate.

The apical region (Fig. 1) is rather obscure owing to the intercalary deposition of calcite having masked the outlines of the plates. There are four gonopores, the posterior pair (in interambulacra 1 and 4) being larger and more widely separated than the anterior pair (in interambulacra 2 and 3). Ocular plates are indistinguishable and no ocular apertures can be seen. The madrepore in interambulacrum 5 is relatively large, broadly elliptical with an adapical acute angle between gonopores 2 and 5, and separates petals I and V, which are therefore not confluent proximally.

The peristome, which is anteriorly placed, below the apical region, presents a transverse crescentic outline when viewed from below, the anterior border being convex; breadth, 34 mm. The mouth, as usual, is directed antero-ventrally owing to the ventral displacement of the labrum.

The periproct is elliptical, situated on the obliquely truncate postero-ventral border of the test, below the ambitus, length 26 mm., breadth 20 mm.

The peripetalous fasciole is typical of Brissids.

The sub-anal fasciole is complete, surrounding a broadly reniform sub-anal plastron. There is no trace of an anal fasciole. As this arrangement is of generic significance, the region of the periproct is shown in Fig. 2. Breadth of sub-anal plastron, 75 mm., height at centre 27 mm.

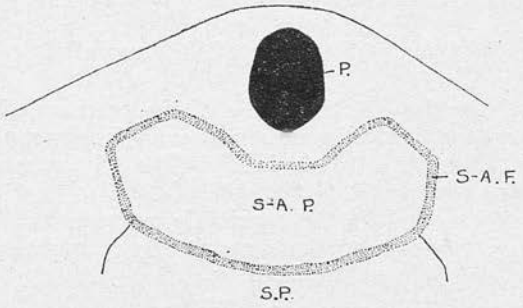

Fig. 2. Region of periproct. P., periproct; S-A.F., Sub-anal fasciole; S-A.P., Sub-anal plastron; S.P., Sternal plastron, x .5.

The sternal plastron is in the form of an isosceles triangle, the base of which is slightly concave and formed by the ventral border of the sub-anal fasciole, and the sides are convex where they border ambulacra I and V, while the apex is truncated by the labrum. The sternum is very obliquely keeled, and is remarkable for showing distinct traces of the radial fan-like furrowing characteristic of the genus *Metalia*. Length 104 mm., greatest breadth (midway along its length), 95 mm.; breadth at base, 65 mm.

Posterior petals, I and V, distinct, not confluent at any point, commencing on either side of the madrepore, and extending postero-laterally half the distance to the ambitus; 75 mm. long, deeply sunken (maximum depth 8 mm.), narrow (maximum width 8 mm.), bearing 40 distinct pairs of pore-pairs, all (except the adapical 3 or 4) approximately equally spaced. There are in addition signs of approximately three obsolete pairs at the proximal end of each petal.

Anterior petals, II and IV, deeply sunken (maximum depth 7 mm.), narrow (maximum width 7 mm.), the proximal two-thirds of each petal directed very slightly posteriorly, so as to form an obtuse angle with ambulacrum III. The distal one-third of each petal curves slightly anteriorly. Length of each petal 70 mm., extending seven-tenths of the meridional distance from the apex to the ambitus. There are 36 distinct pairs of pore-pairs, but as there are approximately five more obsolete proximal sets, the total will be about 41 for each petal.

The anterior ambulacrum III is for the most part flush with the test, save at the ventral extremity near the peristome. There are 32 pairs of solitary pores, some obsolete. The ambulacrum bears a median groove, 2 mm. wide, bordered on either side by a double or triple line of secondary tubercles, so that in general structure it resembles a fasciole; and perhaps performs a ciliary feeding function since it leads directly to the mouth. This ambulacrum is obsolete over a short distance below the fasciole, save for a few pores. The fasciole cuts it some 25 mm. above the ambitus, i.e., approximately two-thirds of the meridional distance along the ambulacrum from the apex to the ambitus. The obsolete section of the ambulacrum is responsible for the absence of an anterior notch from the ambitus.

There is nothing remarkable about any of the interambulacra, save the dorsal and ventral keel of interambulacrum 5, already described.

Systematic Position of Brissus gigas.

It can be seen that the characters of the species so far as can be determined from the test are in accordance with the diagnosis of *Brissus*, quoted above (from H. L. Clark, 1925). The only unexpected feature is the very large size.

On the other hand, if the species is assigned to *Brissus*, some anomaly results from the fact that others of its characters accord better with the genera *Metalia* and *Meoma*.

In a private communication Dr. Th. Mortensen, of Copenhagen, remarks on the general resemblance of the animal to *Metalia*, a genus which sometimes reaches a size approaching that of the present example. Both Ludwig (1904) and Tenison-Woods (1878) have drawn attention to the radial furrowing of the sternum in *Metalia*. The former gives it as the sole distinguishing feature from *Brissus*; but as now recognized, *Metalia* is also characterised by possessing anal fascioles. The latter are lacking in *B. gigas*, and as Mortensen regards this as an important diagnostic feature, it does not seem advisable to place the species in *Metalia*. According to H. L. Clark (1925) a diagnostic feature of *Metalia* is the absence of large primary tubercles from within the peri-

petalous fasciole. *B. gigas* possesses such tubercles, which would also argue against placing it in *Metalia*. On the other hand, Tenison-Woods (1878) has recorded that the Australian species of *Metalia* possess the common feature "tuberculation within the peripetalous fasciole coarse, frequently consisting of primary tubercles." Owing to lack of material it is not possible for the writer to check these discordant statements. According to Jackson (1912) *Metalia* is notable in having both the primary and secondary tubercles perforate. *B. gigas* has only the primary tubercles perforate. Thus the main part of the evidence seems to weigh against assigning the species to *Metalia*, with which in general form, size and furrowing of the plastron it otherwise shows agreement.

The genus *Meoma* possesses a test of size and form comparable to *B. gigas*, and has similarly sunken petals. In this case disagreement occurs in the structure of the sub-anal fasciole, which is complete in *B. gigas*, whereas the diagnosis of *Meoma* given by H. L. Clark (1925) states that the sub-anal fasciole is imperfect, so that there is no well-marked sub-anal plastron. The anal fascioles are absent in *Meoma*, a point in respect of which *B. gigas*, *Brissus* s. s. and *Meoma* all correspond.

Owing to the fact that only the one test is available the species is recorded here under *Brissus*. When more material is obtained it will be possible to see how far the characters of the type specimen are normal ones and to what extent individual variation is involved; the characters of the exoskeleton and internal organs will also have an important bearing. If the characters described above prove to be constant, then it may be preferable to erect a separate genus, the characters of which would probably include the following:—

Test large, wide and inflated, without anterior notch; Peripetalous fasciole and sub-anal fasciole present, but no anal fasciole. Petals well formed and depressed. Sub-anal plastron wide, reniform. Sternal plastron large, bearing radiating fan-like furrows arising from the posterior margin. Primary tubercles extending within the peripetalous fasciole, and only the primary tubercles perforate.

Whether this combination of characters distinctive of various genera indicates a primitive condition or a case of convergence it is not possible at present to say. The large size would seem to count against the possibility of *B. gigas* being a primitive form.

Acknowledgment.

I am indebted to Mr. A. W. B. Powell for the opportunity of reporting on this specimen; and to Dr. Th. Mortensen, of the Copenhagen Museum, who kindly gave his opinion on the generic problem involved.

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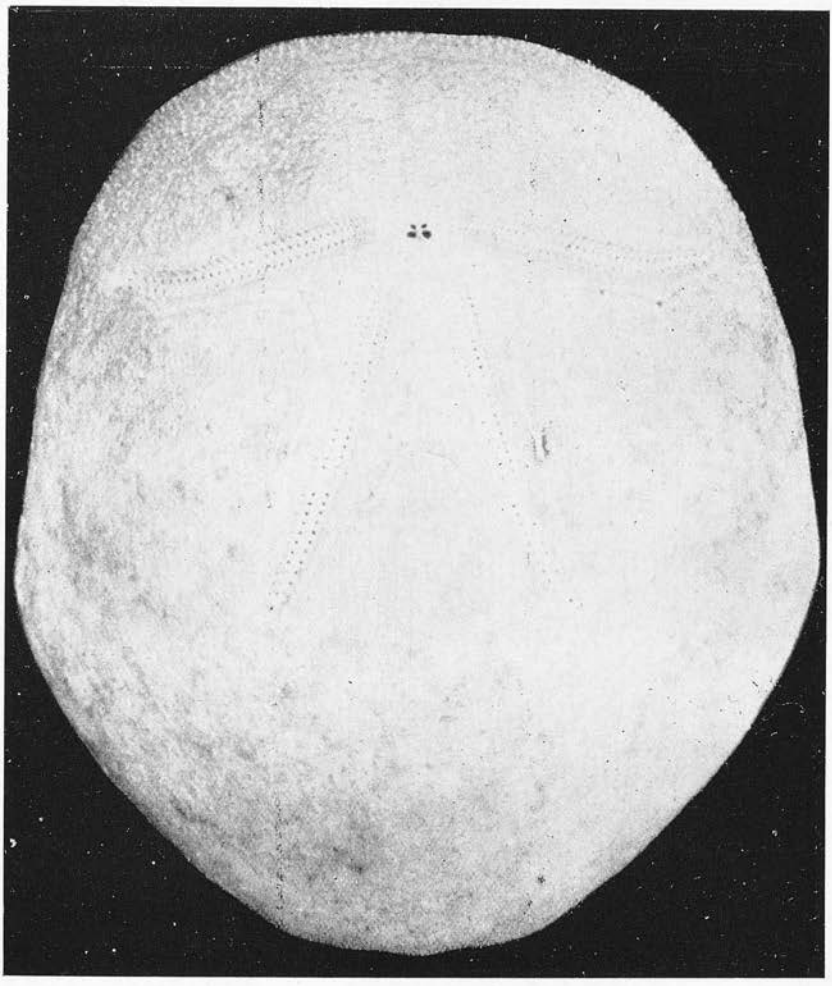
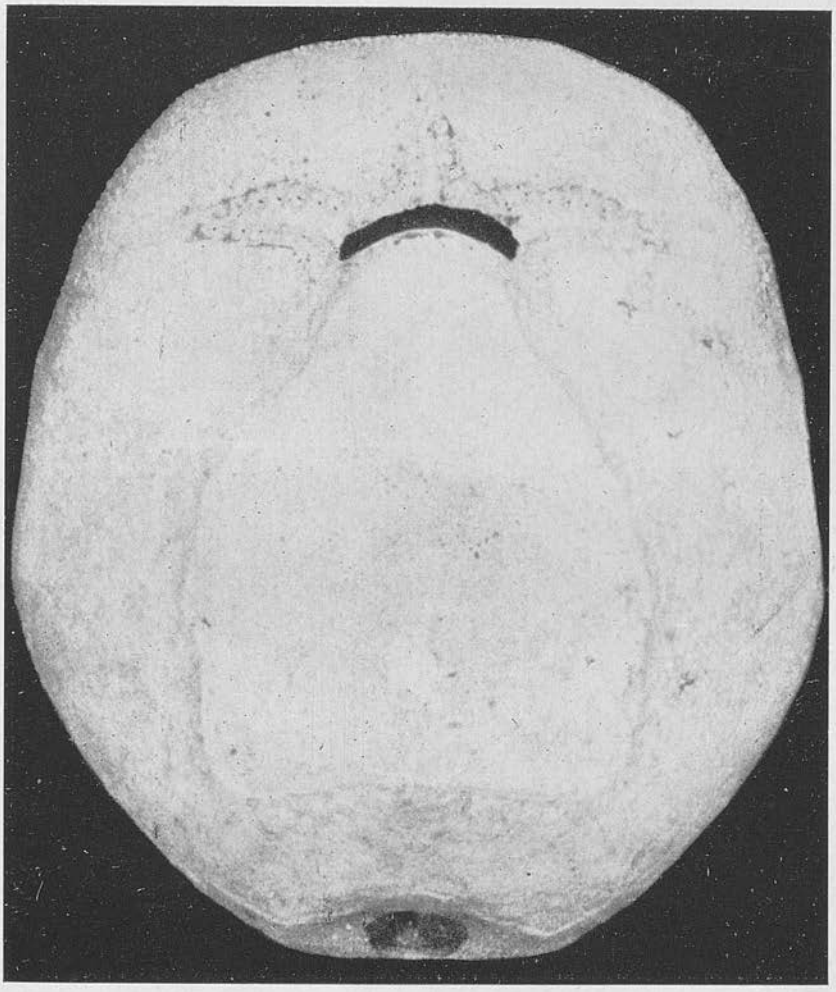


Brissus gigas n. sp. Abactinal view of test x 3/5.



Brissus gigas n. sp. Actinal view of test x 3/5.

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A Triassic Echinoid from New Zealand.

By

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Victoria University College, Wellington.

A Triassic Echinoid from New Zealand

By H. Barraclough Fell, Victoria University College, Wellington

[*Received by the Editor, November 9, 1948; issued separately, February, 1950.*]

Recently some fragmentary remains of a Cidarid were discovered in Triassic strata in Nelson. These represent an undescribed genus and also constitute by far the oldest echinoid remains so far known from New Zealand. The material comprises internal and external natural moulds in indurated argillite. It was collected by Mr H. W. Wellman, of the New Zealand Geological Survey, and submitted to me through the courtesy of Dr J. Marwick.

Order Cidaroidea Duncan

Family Cidaridae Gray

Dicyclocidaris n.g.

Cidarids of medium size, in which the larger interambulacral plates possess two concentric rings of scrobicular tubercles; the outer ring demarcating the boundary of the scrobicule, and the inner ring well within the margin, separated by a greater or lesser interval from the outer. Ambulacral border of the interambulacral plates denticulate. Tubercles perforate, strongly crenulate.

D. denticulata n.sp.

Dimensions: horizontal diameter ca. 20 mm., height ca. 12·5 mm. (estimated from cotype, a broken internal mould). Probably 7 or 8 interambulacral plates to each vertical series.

The holotype constitutes an external mould of four interambulacral plates which seem to comprise the proximal half of a natural series. The description and photographs (Figs. 1 and 2) are taken from positive casts made from the moulds, Fig. 1 being part of the holotype specimen.

Scrobicules shallow, circular on the larger plates, transversely oval on the smaller proximal ones. Scrobicules of the proximal plates confluent, reaching to both the proximal and distal borders of the plates; on the larger plates, no doubt from the ambital region, the scrobicules reach only to the proximal border of each plate, where they are slightly truncated. Tubercles large, prominent, standing well above the general level of the scrobicule, each with about 12 crenulations. Scrobicular tubercles of the outer ring numbering ca. 16 on an ambital plate, and the inner ring comprises about the same number. The inner ring may be separated from the outer ring by an interval only as wide as one scrobicular tubercle, as in the holotype (Fig. 1), or the inner ring may lie midway between the outer ring and the base of the parapet, as in a cotype (Fig. 2). Both scrobicular rings are interrupted by the truncation of the scrobicule at the proximal margin. Tuberculation outside the scrobicule not well preserved, but apparently similar to the scrobicular tubercles in form and size, but irregu-

larly arranged and less distinctly differentiated. The ambulacral border of each interambulacral plate bears on its inner surface 6 or 7 denticulations (Fig. 3, from an internal natural mould).

Ambulacra, peristome, periproct, apex and spines unknown.

Locality: Wai-iti Survey District, Nelson, east side of Castle Hill. Grid reference S20/427097. G.S.4560.

Horizon: Carnic (upper Triassic).

Type and Cotypes: In the collection of the Geological Survey Office, Wellington.

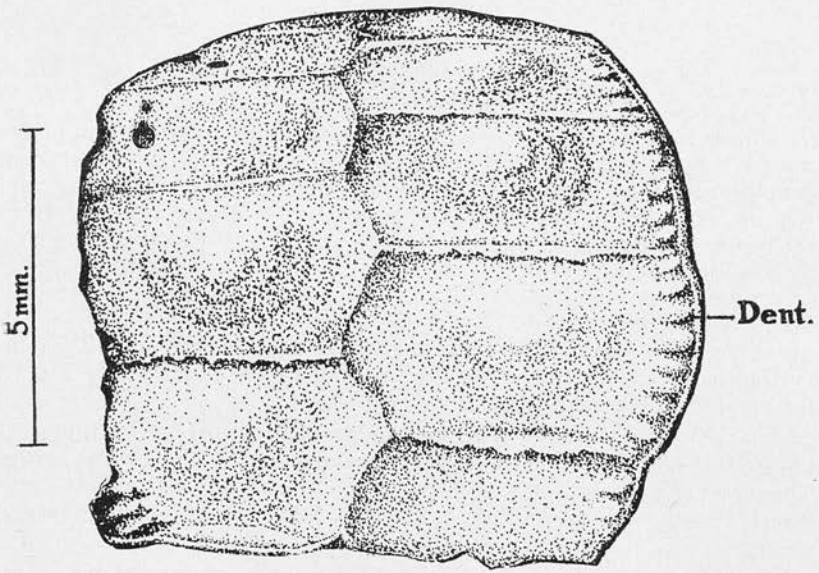


FIG. 3—*D. denticulata*, another cotype, an internal natural mould of part of an interamb, showing impressions (Dent.) left by the denticulate edge of the ambulacral margins of the plates. The ambulacral margins of the left column of plates have been eroded away.

DISCUSSION

No Triassic Cidaridae are known from Australia. The oldest Cidarid from that region is "*Cidaris*" *comptoni* Glauert (1923), from the Cretaceous of Western Australia. This species, whatever its real generic position may be, is certainly unrelated to *Dicyclocidaris*, as the structure of the two forms is not at all comparable.

Of the three subfamilies of Cidaridae recognized by Mortensen (1928), two, namely the Stereocidarinae and Diplocidarinae, are unknown prior to the Jurassic. The remaining subfamily, the Streptocidarinae, ranges from Lower Carboniferous to the Lias in Europe and North America. The special feature of the Streptocidarinae is the imbrication of some of the plates. The material of *Dicyclocidaris* so far obtained is insufficiently complete to determine the presence or absence of this condition. What does appear to be highly significant, however, is the fact that the ambulacral margins of the interambulacral plates are denticulate. This is one of the diagnostic characters of

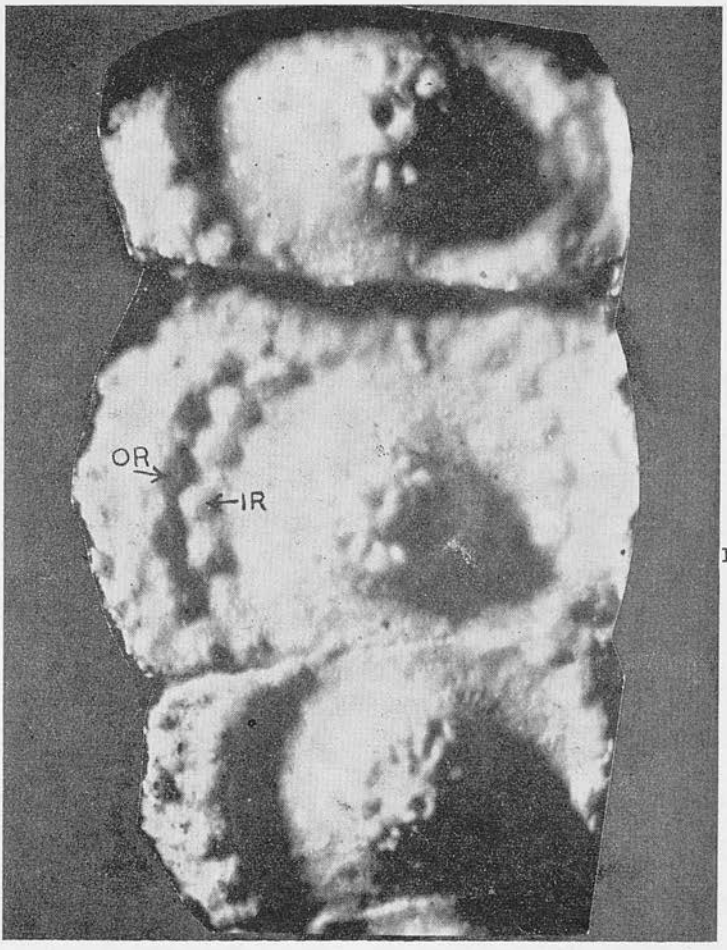
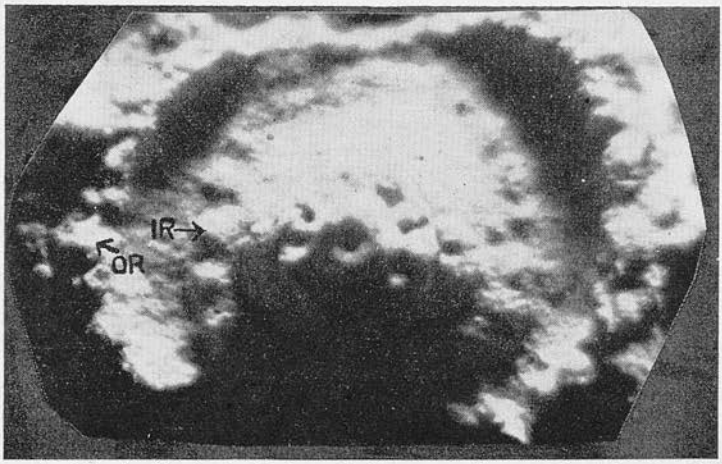


Fig. 1.



5 mm.

Fig. 2.

FIG. 1—*Dicyclocidaris denticulata*, holotype specimen. OR, tubercle of the outer scrobicular ring; IR, tubercle of the inner scrobicular ring. Positive impression taken from original negative external mould. Lower border proximad.

FIG. 2—*D. denticulata*, cotype specimen, showing the inner scrobicular ring relatively further within the margin; abbreviations as for Fig. 1. Positive impression taken from original negative external mould.

To face page 84].

Miocidaris, a genus of Streptocidarinae typical of the Triassic of Europe and North America. There is also a further important parallel between *Dicyclocidaris* and *Miocidaris*. With only one exception, the Cidarids did not develop crenulated tubercles until the Jurassic. The exception is *Miocidaris*, which already had the crenulation developed in the Triassic. To this we must now add *Dicyclocidaris*. The evidence would thus point rather strongly in favour of grouping *Dicyclocidaris* with *Miocidaris* in the Streptocidarinae.

The two genera are mutually distinguishable by the fact that the scrobicular tubercles are monocyclic in *Miocidaris*, dicyclic in *Dicyclocidaris*. Dr Th. Mortensen, of the Copenhagen University Museum, who has examined photomicrographs of the interambulacral casts, makes the following interesting comment on the possible meaning of the inner ring of tubercles, so foreign to the usual conception of Cidarids (private communication, 28/3/48) : "I cannot help thinking of *Porocidaris*, with a circle of *pores* inside the scrobicular ring. Just as these pores in *Porocidaris* are no true pores, I think the inner series of tubercles in your Cidarid are no true tubercles, viz. not spine-bearing, as are the scrobicular tubercles, but only a peculiar structure within the areole. From my knowledge of the Cidarids I should think it impossible that there could have been a circle of spines inside the normal circle of scrobicular spines, these latter lying always directly as a cover of the muscle of the primary spine. I think you have here a new genus forming a close analogy to *Porocidaris*."

If the foregoing discussion is a correct interpretation of the fossils, then it seems that the following conclusion may legitimately be made. As early as the Triassic the echinoid fauna of the New Zealand region contained an element which, although at the equivalent evolutionary stage to that occurring contemporaneously in Europe and North America, nevertheless showed a distinctive Zealanic character of at least generic value. Whether this Zealanic character could more correctly be described as Australasian cannot be determined until something is known of the Triassic Cidaridae of Australia.

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Some Off-Shore and Deep-Sea Ophiuroids from New Zealand Waters

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Zoology Publications from Victoria University College, No. 13
Issued 1st December, 1951

ABSTRACT

Amphiura abernethyi sp.nov., characterized by widely separated radial shields, an almost naked adoral disc, and lateral arm-plates bearing five arm-spines, is described from material trawled in Cook Strait from 50 fathoms. *Ophiactis cuspidata* Lyman, previously known from the "Challenger" dredgings off the Kermadec Islands, is reported from the Tasman Sea, at a point 400 miles north-west of Wellington, where it was taken in 600 fathoms. *Ophiopteris antipodum* Smith is recorded from 400 fathoms, off Timaru; and *Astroporpa wilsoni* Bell from 150 fathoms, off Mercury Bay.

The genus *Amphiura* is represented in the New Zealand fauna by some fifteen species known hitherto, to which is now added a further species from littoral waters of Cook Strait. All but one of the species are endemic to the New Zealand region. Most of them are rather small forms, but three—namely, *Amphiura aster*, *A. rosea*, and *A. norae*—reach or exceed an armspread of 100 mm. Of the latter, *A. norae*, Benham (1909) has hitherto been unique in possessing an almost naked aboral disc surface, with paired tentacle scales. However, both these features prove now to be shared by another large *Amphiura* trawled by Mr. F. Abernethy in Cook Strait; the species is here described as *Amphiura abernethyi* sp.nov. The chief distinction between *A. norae* and *A. abernethyi* may be seen from the following comparisons:—

Amphiura norae

Radial shields separated by an intervening space which is but little broader than the width of one shield, and occupied by five to seven mosaic platelets.

Lateral arm-plates bearing each four arm-spines.

Amphiura abernethyi

Radial shields widely separated, the intervening space occupied by about 25 to 30 polygonal mosaic platelets of varying size.

Lateral arm-plates bearing each five arm-spines, the upper four directed outwards from the arm, the lowermost directed distally, parallel to the axis of the arm.

In addition, there are easily observable differences in the shapes of the radial shields and of the arm-plates, as can be appreciated by comparing Benham's (1909) figures with those given here. Notable is the attenuation of the proximal part of the radial shield in *Amphiura abernethyi* and the curvature of the whole plate, both features not apparent in Benham's figures of *Amphiura norae*.

AMPHIURA Forbes 1842

Amphiura abernethyi sp. nov. (Figures 1–4.)

Dimensions.—Holotype: R, 140 mm.; r, 7 mm.; ratio R/r, 20. The dozen or so syntypes are fragmentary, but suggest that the data given for the holotype are generally true. The holotype is complete.

Colour: Bright orange in life, fading to pale grey in alcohol or after drying.

Disc: Form pentagonal, constricted in the interradii. Aboral surface covered by numerous closely imbricating small scales, among which the original embryonic

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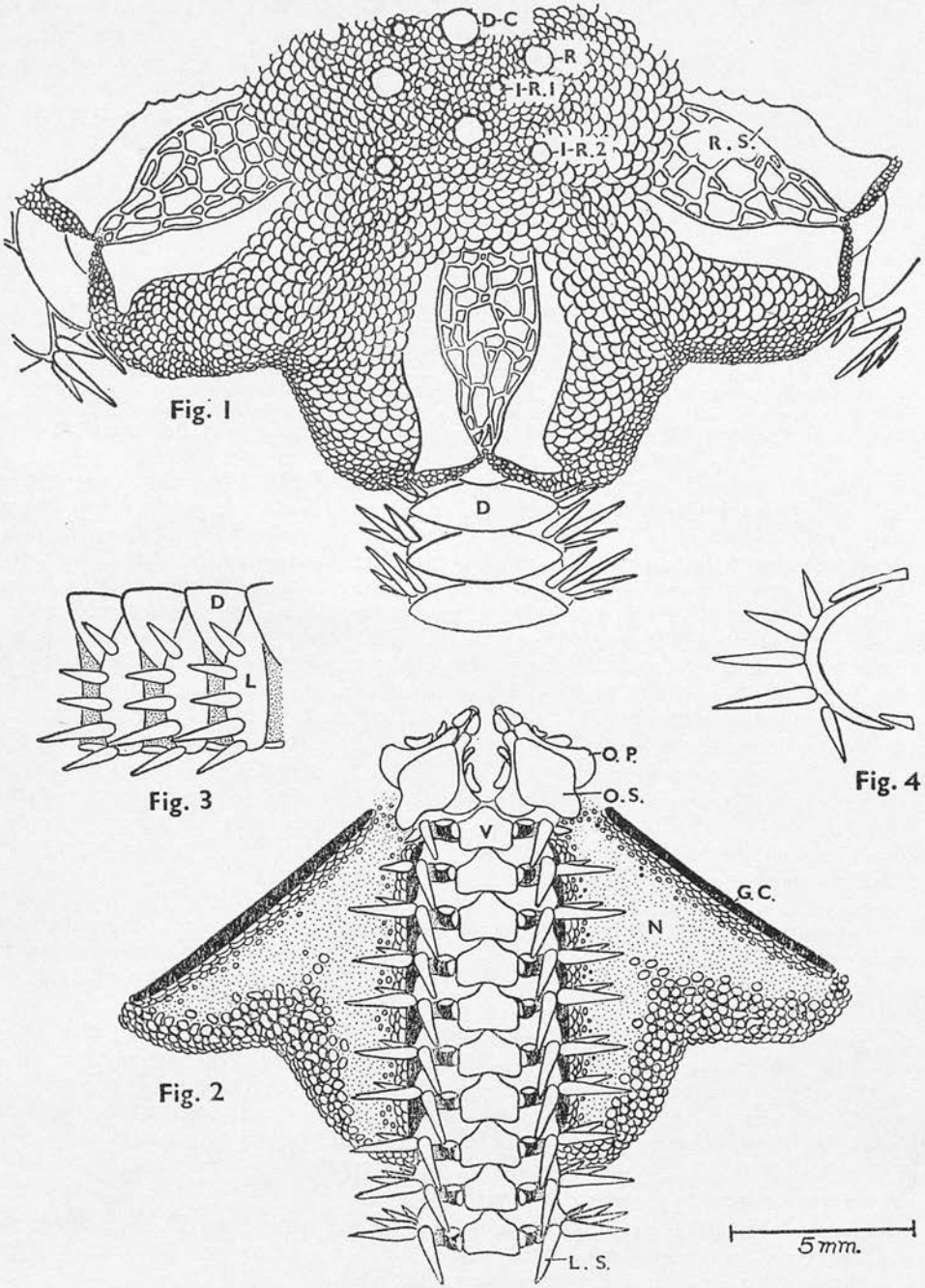

Amphiura abernethyi sp.nov.

Fig. 1: Aboral aspect. Fig. 2: Adoral aspect.
Fig. 3: Lateral aspect of arm, near base. Fig. 4: Arrangement of spines on lateral arm-plate.

Abbreviations: D, upper arm-plate. D–C, dorso-central primary plate. G.C., genital plate. I–R.1, first inter-radial primary plate. I–R.2, second inter-radial primary plate. L, lateral arm-plate. L.S., lowermost arm-spine. N, naked area of disc dermis. O.P., adoral plate. O.S., oral shield. R, radial primary plate. R.S., radial shield. V, lower arm-plate.

primary plates (the dorso-central, radials, first and second inter-radials) remain distinguishable in the central region. The primary plates are widely separated by intervening scaled areas in the adult. Radial shields prominent, about five times as long as broad, widest distally, attenuated proximally, reaching from near the periphery to a point about midway to the centre of the disc. Radial shields widely separated save at their distal extremities, the intervening area between them occupied by a mosaic of about 30 irregularly polygonal platelets, of uneven sizes, which do not imbricate. The proximal abradial borders of the radial shields are partly concealed by imbricating plates of the general disc scalation. Adoral surface incompletely scaled, the dermis being almost naked save for the peripheral part and the margins of the genital clefts. The genital clefts extend almost to the periphery of the disc. Oral shields spearhead-shaped, longer than broad, with an acute angle within. Adoral plates broader without than within, proximally contiguous. The inner and outer pairs of oral papillae larger than the intermediate pair.

Arms: Long and slender, tapering to fine extremities .Upper arm-plates elliptical, their long axes transverse, about three times as broad as long, the distal border of each slightly overlapping upon the proximal border of the next plate. The most proximal plate of the upper series reduced in size, partly obscured by the disc margin. Lateral plates meeting neither above nor below, the more proximal ones bearing five arm-spines, of which the lowermost is directed distad, parallel to the long axis of the arm, the other directed outwards, the second lowermost being the longest. Lower arm-plates five-sided, yet mainly sub-rectangular in outline, owing to the fact that the two disto-lateral angles are blunt right-angles, whilst the proximal angle is exceedingly obtuse; the distal border of each very weakly concave, and weakly imbricating over the proximal angle of the next plate. Tentacle scales two, one attached to the lower arm-plate, the other to the lateral plate.

Holotype; In the museum of the Department of Zoology, Victoria University College, Wellington.

Type Locality: Off Cape Campbell, Cook Strait, New Zealand; trawled from 50 fathoms.

It may be noted that no young were seen in the bursae of dissected specimens, so that the species may provisionally be regarded as oviparous. It seems unlikely that this species could be merely a larger form of *Amphiura norae* (as might be concluded from the fact that it has one more spine on the lateral plates, and more mosaic platelets between the radial shields); the fact that the radial shields are more slender than in the smaller *A. norae*, and the distinctive arrangement of the spines of the arm, both point to the conclusion that *A. abernethyi* is a different species. It appears to be common at the type locality, though it has not been taken at any other point. *A. norae* was originally described from off Cape Kidnappers, and has not with certainty been taken since.

Ophiactis cuspidata Lyman 1879

Specimens referable to this species are in the Dominion Museum, Wellington. They were collected by Mr. W. Foster, of the C.S.S. "Recorder" in 1932, at a point 400 miles north-west of Wellington, in the Tasman Sea, at a depth of 600 fathoms. This species was originally described from material dredged by the "Challenger" from 520 to 600 fathoms, off the Kermadec Islands. It has not, apparently been since seen. Of the other five-armed species of *Ophiactis* known from New Zealand waters, all differ from the present species in so far as the latter has spines on the disc and also two or three oral papillae on either side of the jaw.

Astroporpa wilsoni Bell 1917

Hitherto only the original "Terra Nova" type specimens (now in the British Museum) have been known. It is therefore of considerable interest that another specimen has come to light. It was taken by a fisherman off Mercury Bay, Coromandel Peninsula, and secured by Miss U. V. Dellow, who kindly forwarded it. It is said to have been adhering to a fishing-line and to have been brought up from 150 fathoms, a statement not inconsistent with the submarine contours off Coromandel, nor with the general abyssal facies of the genus. It was attached to a portion of gorgonid coral.*

The distinctive features of *Astroporpa wilsoni* and a key to the Gorgonocephalidae are given elsewhere (Fell, 1949).

Ophiopteris antipodum E. A. Smith 1877

A specimen of this striking species was taken in 40 fathoms, off the coast of Timaru, South Island, by Miss P. M. Ralph in February, 1951. Its distinctive feature is the possession of supplementary scale-like spines over the arm-spines. It is endemic to New Zealand, one other species being known from California. This is the most southern record, it being known previously only from Cook Strait and from Rangitoto Island. Despite its relatively wide distribution in New Zealand waters, it is nevertheless rarely seen.

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*Identified as *Paracis* sp., by Miss P. M. Ralph, who will be recording the specimen elsewhere.

With the Author's Compliments.

THE OCCURRENCE OF AUSTRALIAN ECHINOIDS IN NEW ZEALAND WATERS

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From Rec. Auck. Inst. Mus. Vol. 3. No. 6, pp. 343-346, 21st December, 1949.

The Occurrence of Australian Echinoids in New Zealand Waters

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Abstract.

Clypeaster australasiae is recorded for the first time from New Zealand. The species *Holopneustes inflatus* and *Centrostephanus rodgersii*, though reported from New Zealand over fifty years ago, were subsequently deleted from the faunal list for lack of reliable evidence. Accurate localities are now given for specimens taken alive, and also for other material in unmacerated condition, with adherent spines and pedicellariae. The new evidence invalidates the theory recently proposed by H. L. Clark (1946) that New Zealand records of *Holopneustes inflatus* are attributable to dead material of Australian origin which has drifted across the Tasman Sea on floating kelp. All three species must be recognized as true members of the New Zealand fauna. Since two of them are also known from Lord Howe Island, their geographical range probably corresponds to the shallow water boundaries of the Tasman basin on its western, northern and eastern margins.

REGULARIA

Family DIADEMATIDAE

Genus CENTROSTEPHANUS Peters, 1855.

Centrostephanus rodgersii (A. Agassiz)

1863. A. Agassiz, *Proc. Acad. Nat. Sci. Philadelphia, 1863*, p. 354.

Localities: Off Cavalli Islands, south of Whangaroa, in from 70 to 110 metres, two large specimens collected alive in July, 1949; also from Stephenson's Island, Whangaroa, several specimens collected about the year 1925 by the late W. La Roche, though apparently not hitherto placed on record. A specimen from each of these localities is in the Auckland Museum.

The dimensions of the Stephenson's Island example are as follows: Horizontal diameter of test, 97 mm.; height of test, 48 mm.; peristome, 38 mm.; apical system, 21 mm.; longest spines, 45 mm.; number of plates to each column, A 28, IA 16. The largest specimen listed by Mortensen (1940) measures h.d. 95 mm., height 45 mm. However, the late H. L. Clark (1946) has recorded that Australian specimens reach 100 mm. h.d., or more.

The test is pale cream; the spines have the deep purple coloration characteristic of the species. The spines and skin of one of the Cavalli Island specimens are very strongly pigmented, approaching black.

C. rodgersii was first reported from New Zealand by Farquhar (1897) on the basis of a specimen in the then Colonial Museum; he was unable to cite the locality from which it was obtained, and stated that the specimen fell to pieces on its removal from its case. Hutton (1904) omitted the species from the *Index Faunae Novae Zealandiae*, but

Farquhar (1907) corrected this error. Mortensen (1921) again dropped the species from his revised list of New Zealand echinoids, and subsequently (1940) maintained this view. As the evidence for its New Zealand occurrence is now conclusive, the species must be restored to the faunal list. The geographical range of *C. rodgersii* as known so far comprises eastern Australia, Lord Howe Island and New Zealand.*

Family TEMNOPLEURIDAE

Genus HOLOPNEUSTES L. Agassiz, 1841.

Holopneustes inflatus Lütken

1872. Lütken, in A. Agassiz, *Bull. Mus. Comp. Zool.*, 3, 56.

This echinoid has recently been obtained in some numbers from the North Auckland peninsula, and as far south as Great Barrier Island. It is represented in a number of New Zealand collections. Auckland Museum possesses the finest specimen I have seen; it was taken at Houhora Heads in August, 1934, the depth not being recorded. It is of the *purpurescens* form (vide Mortensen, 1943), in perfect condition, and obviously alive when collected. It measures ca. 60 mm. h.d., and 40 mm. in height. The densely arranged spines measure individually up to 5 mm. in length, and are of a delicate, translucent mauve colour, paler at the distal extremity of each. The spines about the peristome are somewhat flattened, a feature which does not seem to have been reported in Australian specimens. Owing to the shortness of the spines, the tube-feet show up prominently as ten narrow, meridional bands, buff in colour, harmonising well with the mauve spines. This, indeed, must be one of the most beautiful sea-urchins of our fauna. The characters of the ambulacral plates, including the trigeminal arrangement of the pore-pairs, the occlusion of the lower element from the outer border of each amb-plate, and the tuberculation of the inter-amb plates, all correspond with published descriptions of Australian material.

Another large, but almost naked, test of 50 mm. h.d. was collected by A. W. B. Powell at Tryphena, Great Barrier Island, in ca. 30 metres. This carries a few spines and pedicellariae. Some 16 specimens, several with abundant spines and pedicellariae, were collected by Gladys Mumby from sandy beach at Doubtless Bay; these are in the Dominion Museum, and others from the same collector are in the museum of the Correspondence School, Wellington, and in the writer's collection.

H. inflatus was first recorded from New Zealand by A. Agassiz (1872), though omitted from the *Index* by Hutton (1904). This is surprising, since Hutton himself obtained a specimen (which he originally described as *"Echinus elevatus"* in 1872)—this specimen being still preserved in the Dominion Museum. Mortensen (1921) restored the species to the faunal list on the basis of a naked test taken by Bollons at Little Barrier Island, but subsequently (1943) he has treated the

* Since the above was written Mr. A. W. B. Powell obtained a living specimen from a trawl on the edge of the Centre Reef, Hauraki Gulf; 5½ miles S.E. of Little Barrier Island, 25-28 fathoms.

matter as uncertain. H. L. Clark (1946) regarded the occurrence of bare tests as providing no evidence of the species' occurrence, as he thought dead tests might be transported long distances on floating kelp. He concluded: "It is quite improbable that either *Amblypneustes* or *Holopneustes* lives in New Zealand seas."

The character of the material recorded above can leave no further grounds for maintaining such an opinion. The species is therefore to be retained on the faunal list. Its known geographical ranges comprise south and eastern Australia, Tasmania and New Zealand.

It is worthy of note that Farquhar (1926) recorded *Amblypneustes pachistus* (under the name *A. ovum* var. *pachistus*) from New Zealand. Since he is now proved correct in the cases of *C. rodgersii* and *H. inflatus*, there is strong reason to accept his report of *A. pachistus*.

IRREGULARIA

Family CLYPEASTRIDAE

Genus **CLYPEASTER** Lamarck, 1801.

Clypeaster australasiae (Gray)

1851. Gray, *Proc. Zool. Soc., 1851*, p. 34.

Specimens recently dredged by A. W. B. Powell from 157 metres, off East Cape, and also off Parengarenga in from 70 to 90 metres, are all referable to this species. They are located in the Auckland Museum.

Australian specimens show considerable variation in the shape of the test, as discussed by Mortensen (1948), and a corresponding variation is apparent from the dimensions of the three New Zealand examples submitted to me.

Specimen.	Length.	Breadth.	Height.	Length of Spines. Aboral.	Adoral.
A	116 mm.	104 mm.	32 mm.	3 mm.	1-2 mm.
B	99 mm.	90 mm.	32 mm.	3.5 mm.	1-2 mm.
C	92 mm.	84 mm.	23 mm.	3 mm.	1-2 mm.

Note.—Specimen C has a depressed apical region.

This is the second species of *Clypeaster* to be reported from New Zealand, and the first for which an accurate locality and depth is available. The other is *C. virescens* Doderlein, of which H. L. Clark (1925) recorded two specimens in the British Museum labelled "from off New Zealand (Terra Nova)." Bell (1917), in the official report on the *Terra Nova* echinoderms, had included no reference to such specimens.

KEY FEATURES.

To facilitate the recognition of any other specimens of these echinoids which may be obtained locally, the following characters may serve to distinguish them from other New Zealand species.

Centrostephanus rodgersii is at once recognizable by its large, robust test, its long, tapering, hollow spines, and deep purple colour.

Holopneustes inflatus is characterized by its almost spherical test, rarely exceeding 50 mm. in diameter, and by its dense coating of numerous short, red, bristle-like spines. In the case of the form purpurescens, the test may be larger, up to 70 mm. or so diameter, and the spines are mauve or purple. The large forms are more nearly hemispherical than the smaller ones.

The two species of **Clypeaster** are superficially similar; both are flattened shield-urchins, of oval or sub-pentagonal outline, with the aboral surface raised sub-conically, and bearing five petaloid ambulacra with the pore-series distally unclosed. **C. australasiae** has a concave lower surface, and 6-9 tubercles occur on each transverse costa between pore-pairs, the tubercles of the more distal costae being arranged in double series, while those of the remainder are in single series. **C. virescens** has a more nearly flat adoral surface, and not more than four tubercles occur on each costa, always in single series.

ACKNOWLEDGMENTS.

I have to thank Mr. A. W. B. Powell, Assistant Director of the Auckland Museum, for the opportunity to examine and report upon the material. Mr. R. Sharell, of the Correspondence School, Wellington, has also been responsible for assembling material of *H. inflatus*, and his co-operation is gratefully acknowledged.

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TERTIARY AND RECENT ECHINOIDEA OF NEW ZEALAND

CIDARIDAE

By
H. BARRACLOUGH FELL
Victoria University College, Wellington

1954

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Tertiary and Recent Echinoidea of New Zealand: Cidaridae

GENERAL

INTRODUCTION

THE Cidaridae are a group of globe-shaped sea-urchins, remarkable alike for their ancient lineage and for their exceptional symmetry and beauty. The group arose in the late Paleozoic, and reached a peak of development in northern seas during Jurassic and Cretaceous times. Thereafter, in Europe, North America, and in the Mediterranean and North Atlantic areas, the Cidaridae waned, playing no significant part in Tertiary faunas after the Eocene. In New Zealand and Australia, on the other hand, they continued to flourish unabated, and, though very little is known about Mesozoic forms, Tertiary representatives have been found in Australasia of not fewer than one-third of all known Cenozoic genera of the world. The importance of these forms is greatly enhanced by the fact that Australasian Tertiary Cidaridae exhibit clear relationships with Recent forms, whereas the Tertiary Cidaridae of Europe and North America are in the main of obscure relationship and have had to be referred to special fossil " genera " of doubtful taxonomic significance. Broadly speaking, the Australasian Tertiary Cidarid faunas are the richest so far known, though it seems likely that when the Tertiary formations of northern India and Indonesia are more fully explored, theirs will ultimately prove to be the richer yield; for, as argued in this work, it was probably by way of India and Indonesia that the majority of the Cidarids came to Australasia.

New Zealand's Cidarid faunas were at their richest during mid-Tertiary times, when there existed magnificent species, in size and aspect recalling the largest known tropical and sub-tropical forms of the Recent Indo–Pacific. In generic composition the New Zealand mid-Tertiary faunas resembled those of Australia. With the onset of the cooler Pliocene, however, the New Zealand Cidarids (and other echinoids) dwindled, and cool-water echinoids of a different aspect took their place. At the present time only two Recent species of Cidarids are known to inhabit New Zealand off-shore waters. Much of Australia, on the other hand, seems to have remained habitable by Cidarids during the Pliocene, with the result that when water temperatures began to rise again in Recent times the old stock was able to move southwards and recolonize most of the coastal waters. Thus, the Recent fauna of New Zealand has lost its former resemblance to that of Australia.

Cidarid plates and radioles are usually sufficiently robust to endure as fossils, or at least to leave a clear impress of their shape and surface sculpture. This, taken together with the fact that Cidarids have been an important element in Indo–Pacific littoral faunas since the Mesozoic, makes the group a significant one in Australasian paleontology. In the present account of New Zealand Tertiary and Recent Cidarids an attempt is made to meet two requirements. Firstly, to provide an adequately illustrated systematic account of the material, together with a discussion of the relationships of the faunas, their origins, and their migration routes. Secondly, to furnish the field paleontologist with a ready means of recognizing, and therefore using, the fossils which he encounters. The long delay in employing Tertiary echinoids in New Zealand paleontology is attributable to the difficulty experienced in identifying them. Thus, to make the work as widely useful as possible, keys have been included, together with a short illustrated glossary of the essential technical terms.

All New Zealand Tertiary Cidarid material known to exist in public and private collections has been examined during the course of the work. I am indebted to the Directors of the following institutions for the loan of collections in their care: The Geological Survey of New Zealand, Auckland Institute and Museum, Dominion Museum, Canterbury Museum, and the Geological

Department of Otago University. The Director of the National Museum of Victoria, Melbourne, generously lent some important Australian type material for comparison with New Zealand forms. I also acknowledge the help and advice of Dr J. Marwick, then Senior Paleontologist of the New Zealand Geological Survey, and of Dr C. A. Fleming, the present Senior Paleontologist. The late Dr H. J. Finlay determined the age of Foraminifera from several matrices. For various kindnesses I am grateful to the following: Dr R. A. Falla; Mr A. W. B. Powell; Professor B. J. Marples; Professor L. R. Richardson; Professor R. S. Allan; Mr H. W. Wellman; the late Mr F. Hutchinson; Professor W. N. Benson, F.R.S.; Mr A. G. Brighton, of the Sedgwick Museum, Cambridge; Mr R. T. M. Pescott and Mr R. A. Keble, of Melbourne; Mr D. Hamilton; Dr L. Bairstow, who arranged for the return to New Zealand of collections formerly sent to the British Museum; Mr G. Turner, who made special collecting trips at my request; the late Mr A. C. Amies; and Mr J. R. Ower. The collectors of specimens, where known, are mentioned under the entries for the species concerned. I am particularly indebted to the late Dr Th. Mortensen, of Copenhagen, for advice and encouragement over a number of years. To Miss A. M. Clark, of the British Museum, and to Lieutenant-Commander F. Ziesenhenne, of the Allan Hancock Foundation, California, I am grateful for valuable exchange material for comparative purposes. The photographs on Plates 12–14 were taken by Dr J. T. Salmon, A.R.P.S., of Victoria University College. The study has been carried out in the Zoology Department of Victoria University College, with the aid of a research grant from the University of New Zealand.

HISTORICAL SKETCH

Although very little has hitherto been published on New Zealand fossil Cidarids, much of the material described here was collected many years ago. Indeed, some of the best specimens in the collection of the New Zealand Geological Survey were obtained by Alexander McKay during the seventies and eighties of the last century. The following sketch summarizes previously published work on the subject, and also attempts to trace how the existing collections came into being. The principal sources of information have been the *Reports of Geological Explorations* and the *Index of Fossiliferous Localities* of the old Colonial Museum and Geological Survey, during the period of Sir James Hector's directorate.

The first account of fossil echinoderms from New Zealand is that of Zittel (1864), who described and illustrated five species (none of them Cidarids) collected by Hochstetter during the visit of the Austrian frigate *Novara*.

Hector visited the Weka Pass in 1867, and Haast in 1869. They are known to have collected fossils, but whether any of the Cidarids which now bear the locality number 74 were collected by them cannot now be determined. Although no reference to Cidarids is made in Haast's (1871) account, it is possible that some of the old Weka Pass material of *Phyllacanthus titan* now in the Canterbury Museum may have been collected by Haast.

The first published reference to a Cidarid is that of Hutton (1873), who described *Cidaris striata* from Brighton, south-west Nelson. The species, though unrecognizable from his description, is still represented by the holotype in the collection of the N.Z. Geological Survey, and Hutton's specific name may therefore be retained. It is here referred to the genus *Stereocidaris*.

McKay (1877a) recorded a collecting visit to the Weka Pass which he made in 1874. Although he did not mention Cidarids or other echinoids, it is probable that plates and spines of *Phyllacanthus titan* and *Histocidaris mckayi* in the N.Z. Geological Survey collection bearing the locality number 74 were collected then.

McKay (1877b) visited Oamaru in December 1876, collecting at various localities. Although no reference to them is made in his paper, it appears from the *Index of Fossiliferous Localities* that a large series of well preserved radioles of *Phyllacanthus titan* was obtained at Hutchinson's Quarry (GS 172).

In 1879 both McKay and J. D. Enys made collections in the Trelissick Basin. McKay (1881a) listed " *Cidaris* plates and spines " from localities GS 241 and GS 243. Specimens from GS 243 in the Dominion Museum are referable to *Histocidaris mckayi*.

In 1879 McKay also made extensive collections from Curiosity Shop, Rakaia. This locality had previously been visited by Haast (who may be the collector of three radioles of *Stereocidaris*(?) now in the Canterbury Museum), but McKay's fine series of Cidarid remains assembled on this occasion is the best ever made there. In his report, McKay (1881b) mentioned " numerous spines, of which a considerable collection was made. Amongst the latter are many examples of a large smooth spine having a fibrous radiate structure, similar to that seen in the guard of a belemnite. Of this particular fossil one perfect example was found, all others being broken, in length ranging from one to three inches ". It is clear from the description that McKay is referring to *Phyllacanthus titan*, the large radioles of which somewhat resemble a belemnite. Only a few spines of this species now exist bearing the locality number 311 (corresponding to this visit). The perfect specimen mentioned by McKay is not one of them, and it is regrettable that he did not give its dimensions. On the other hand, a large series of radioles of the same species exists, labelled 172, indicating that they were collected by McKay at Hutchinson's Quarry in 1876 (see above). Since he was sufficiently impressed by the large radioles at Curiosity Shop to mention them particularly in 1881, it seems odd that he made no comment on the large series he apparently collected at Hutchinson's Quarry three years earlier. It is possible that the Curiosity Shop series, or a part thereof, somehow received the wrong locality number, 172 instead of 311. Luckily, however, *Phyllacanthus titan* has since been collected at both localities (which are of different age), so that if any error in labelling has occurred it does not affect the known time range of the species.

In the same report, McKay (1881b, p. 82) listed material collected at the Curiosity Shop, GS 311, as follows:

" Spines of Echinodermata with radiate fibrous structure

,, ,, ,, smooth
,, ,, ,, fluted
,, ,, ,, tuberculated
,, ,, ,, thorny
,, ,, ,, branching
,, ,, ,, expanding to cup at top."

The first of these is *Phyllacanthus titan*, as already stated. The last two types are clearly *Goniocidaris hebe*, which is abundant at the locality. The remainder no doubt correspond to radioles, which are here provisionally referred to *Stereocidaris striata*. McKay, who was neither a paleontologist nor a zoologist, is the only person in New Zealand who has hitherto troubled to pay attention to fossil echinoid spines and to record his observations. The collections he made are unrivalled. Although his material has lain unnamed and undescribed for over seventy years, he must be regarded as the real pioneer in the study of New Zealand fossil Cidarids.

In October 1880 McKay was again in the field, this time at the Waihao Forks, where he spent a month with James Park collecting fossils. In his report (1882, p. 70) he referred to " a large form of *Cidaris* ". This was the last and most striking of his Cidarid discoveries, the magnificent species described in this bulletin as *Histocidaris mckayi*, of which he found several large and relatively well preserved pieces of the test. He had, no doubt, previously collected small isolated fragments at the Weka Pass in 1874. He believed that the " radiately fibrous " spines he had earlier mentioned belonged to the same species; but, as already stated, they are referable to *Phyllacanthus*.

The first (and only) illustration of a New Zealand fossil Cidarid appeared in 1886—a small copper engraving of " *Cidaris* from Waihoa " [Waihao] in Hector's *Outline of New Zealand Geology* in the catalogue of the geological exhibits in the New Zealand Court in the 1886 London Exhibition. Though the crudity of the illustration precludes identification, there can be little doubt that it represents one of McKay's specimens of *Histocidaris mckayi*.

Hutton (1888) listed four echinoderms " lately obtained from the Cobden Limestone ", but none of them is a Cidarid.

Tate (1894) mentioned a Cidarid, *Rhabdocidaris*, from the Waihao River. The locality, together with his reference to crenulated tubercles, show that he had a specimen of McKay's *Histocidaris*, but he did not describe it or give it a specific name. *Rhabdocidaris*, essentially a Jurassic genus, is unrepresented in any New Zealand collection.

The echinoids in the collection of the New Zealand Geological Survey were still on exhibition in the Dominion Museum in 1911. When Dr D. G. Lillie visited New Zealand with the British Antarctic Expedition in 1913, he arranged for the collection to be sent to Britain for study and description. It was transferred to the British Museum in 1915, and remained there until 1948, when it was returned to New Zealand. Professor H. L. Hawkins had examined the holotype of *Cidaris striata* Hutton while it was in London, and discussed its relationships in a letter published by Mortensen (1925). Hawkins also mentioned that he had recognized radioles probably belonging to *Goniocidaris* and to *Phyllacanthus*. Otherwise, nothing seems to have resulted during the long period the collection was in England.

In recent years collectors have been active in the field, but the only addition to the fossil Cidarids so far published is *Dicyclocidaris denticulata* Fell 1950, found by H. W. Wellman in Carnic (upper Triassic) rocks in Nelson. The genus is unlikely to have survived the Mesozoic and so has no direct bearing on the present study.

Apart from occasional references to " spines and plates of *Cidaris* ", no other information seems to have been published. This is rather extraordinary since, as the foregoing review shows, material has been accumulating over a period of more than eighty years.

CLASSIFICATION

In the course of the past thirty years a new classification of the Echinoidea has been introduced by Mortensen in which much greater value is placed on pedicellariae as diagnostic structures. This procedure initially met with great opposition, and was flatly rejected by Lambert and Thierry, but at the present time it is generally admitted that it represents the closest approximation to a natural classification so far achieved. It has, however, introduced very serious difficulties for the paleontologist, who is seldom able to secure fossil material with pedicellariae attached.

Before the evidence of paleontology can be employed in such studies as zoogeography, the origin and migrations of faunas, paleoecology, and the like, it is essential to know whether the classification of fossil forms coincides with that of their living representatives—and, if not, how the two differ. The question is of primary importance at the generic level. Unless the fossil forms can be referred to genera which are of substantially the same value as living genera, they cannot be employed for any other purpose than that of merely indexing stratigraphical horizons. If a fossil form is referred to a modern genus on inadequate grounds, the information is liable to be misinterpreted by other workers, who may draw false conclusions from it.

Particular attention has been paid to this problem during the present study. The generic determinations here offered are believed to express much the same relationship as would have resulted from generic determinations made on Recent material instead of fossils. However, not all of the New Zealand material discussed here is amenable to systematic analysis, and some of it is equivocal. Therefore it has been necessary to disregard certain species when making the inductions in the two following sections. It is desirable here to specify the degrees of reliance that may be attached to the various generic placings.

In *Phyllacanthus* there are massive, cylindrical radioles with a characteristic (and diagnostic) fan-like arrangement of the internal lamellae of the stereom. The scrobicular tubercles of the coronal plates offer peculiar features also diagnostic of the genus. The abundant material of *Phyllacanthus*

titan, although fragmentary, is more than sufficient to confirm that that species is correctly grouped with the living forms at present referred to *Phyllacanthus*. *P. wellmanae* is known only from the holotype test, but is clearly congeneric with *P. duncani* of Australia.

Goniocidaris presents characteristic transverse and vertical sutural grooves or pits on the test, whilst the cups, trumpets, and spurs of the primary radioles are equally important diagnostic features. Pedicellariae here, even in living forms, have not been found to have diagnostic value. The fossil species here referred to *Goniocidaris* are at least as closely related to living species of that genus as are the living species to one another.

The primary diagnostic character of *Eucidaris*, on the present conception of the genus, is a terminal crown on the radioles, surrounding a central prominence. The feature is distinctly shown in both of the New Zealand fossil species referred to the genus.

The remaining genera dealt with in the present work are less distinctive, and will have to be considered species by species.

Notocidaris vellai is so placed chiefly because it has spearhead-shaped oral primaries and oblique pores—not conclusive evidence. It has nevertheless been included in the zoogeographic section of this work, for the following reasons: (1) If it has been correctly diagnosed, it represents an Antarctic or Subantarctic element in the Nukumaruan (middle Pliocene) fauna. As no other New Zealand Cidarid is known to have clear southern affinities, to omit this one species would completely suppress important information. (2) If, on the other hand, the species is wrongly placed in *Notocidaris*, to include it in the zoogeographic sections would not materially falsify the aspect of the Tertiary Cidarid fauna, for an overwhelming majority of species have clear Indo–Pacific affinities. The character of the Cidarid fauna as a whole would not be altered by the mistaken inclusion of one southern genus. Moreover, Fleming (1949) has already given independent evidence of the entry of southern elements into New Zealand seas during a cool Nukumaruan phase, so no serious misconception can arise in the present instance.

In *Stereocidaris striata* there are sutural characters, reduced upper areoles, and high interambulacral plates, together with the more generalized Stereocidarine characters—all indicative of *Stereocidaris*—so that its systematic position is reasonably certain. *Stereocidaris hutchinsoni*, on the other hand, is known only from fragmentary remains, both radioles (which are very abundant) and plates (which are very rare). Under the description of the species (p. 36) some reasons are offered for placing it in *Stereocidaris;* but, at best, the classification is only a reasonable guess, and certainly cannot be relied upon.

Histocidaris mckayi is so placed with some confidence for reasons, admittedly somewhat indirect, which are given under the description of the species (p. 32).

The remaining two species, *marshalli* and *haasti*, are tentatively referred to *Prionocidaris*. The species themselves are fairly well characterized on spine structure, but until the spines can be correlated with tests their generic status will remain uncertain. Their spines do resemble, however, those of the Australian Tertiary species *Prionocidaris scoparia*, and no closer relationship to any other genus is evident.

Summarizing, the species *Stereocidaris hutchinsoni*, *Prionocidaris marshalli*, and *P. haasti* should not be utilized in any investigation which presupposes that they are correctly classified, until better information is available. The other species, however, are believed all to be placed in their proper genera.

The importance of fossil echinoid radioles in paleontology has been debated. Hawkins is one of those who have taken a pessimistic view. Referring to some supposed *Phyllacanthus* fossil radioles from Fiji which he thought very like those of *Phyllacanthus imperialis*, Hawkins stated (1934, p. 159): " But the taxonomic value of a cidarid radiole (at least in fossil material) is very slight, and, though I still consider these to represent a true *Phyllacanthus*, I lay no stress on their resemblance to those of the living species ". He gave no other reason for his belief that the spines were referable to *Phyllacanthus*, however, and made no reference to their internal structure.

H. L. Clark (1945) also studied Fijian fossil Cidarids, including the same specimens which Hawkins had discussed. Clark remarked (1945, p. 313): " Hawkins, who examined similar spines, says ' In size and all visible characters these radioles are very like those of *P. imperialis* ', but he adds that he lays ' no stress on their resemblance to those of the living species ' ". After comparing Hawkins' material with that in his own collection, Clark could see no ground for doubting that all should be referred to *P. imperialis*.

Here are two extreme views of the same specimens. Hawkins considered that they were referable to *Phyllacanthus*, but gave it only as his opinion, discarding as of no account their " resemblance " to a living species of that genus. Clark, on the other hand, assigned the specimens to the living species itself, *Phyllacanthus imperialis*. Both appear to have overlooked Mortensen's detailed studies (1928) on the internal structure of Cidarid radioles, and in particular they ignore the fact that a ground transverse section can easily show whether or not a given radiole is referable to *Phyllacanthus*. Other Cidarid radioles have well defined microscopic diagnostic structures, and some radioles also have external sculpture of diagnostic value, for example, *Eucidaris* and *Goniocidaris*. Although the generic determination is the more important for derived studies, specific determinations may also be made from spines if the latter show special peculiarities. Thus, many living species may be recognized at a glance from a single radiole.

Little seems to have been done in continuation of Mortensen's studies on radiole structure, but so far as my own work is concerned, his diagnoses have proved to be well founded. If Mortensen's work be accepted—as surely it must be—it follows that a fragmentary radiole exhibiting diagnostic internal detail or diagnostic sculpture will provide as sound a basis for taxonomic classification as any other portion of a cidarid skeleton. The great advance in stratigraphy in recent years reflects the fruitful employment of microfaunal evidence which was previously ignored. Isolated, even fragmentary, radioles can provide valuable information. They should be regarded as legitimate material in taxonomic paleontology and are so employed in the present study.

ZOOGEOGRAPHIC RELATIONS OF NEW ZEALAND CIDARID FAUNAS

AUSTRALIA

Australian Tertiary Cidaridae were described by Chapman and Cudmore (1934), whose work, with a few amendments, has been accepted by H. L. Clark (1946). There have since been several attempts to achieve a better correlation of the Australian Tertiary column, notably those of Singleton (1941), Crespin (1943), and Finlay (1947). These are in fairly close agreement, though there is a difference of opinion as to the position of the Janjukian. In 1952, Raggatt and Crespin proposed an upper Eocene age for the Janjukian; but, without prejudice to their views, Finlay's correlation is followed in this bulletin. Finlay regarded the Janjukian as either upper Oligocene or lower Miocene. Chapman and Cudmore's records of time-ranges require some modification. The detailed locality data they gave has been converted by Dr Marwick to current Australian stratigraphic terminology (pers. comm. 21 May, 1948). In his paper, Finlay (1947) did not deal with the lower Aldinga beds. He subsequently examined Foraminifera from them, and informed Marwick that they are of upper Eocene age (Marwick, pers. comm. 21 May, 1948).

Stereocidaris australiae (Duncan). Chapman and Cudmore (1934, p. 130) stated that this species ranges from upper Oligocene to Miocene, and H. L. Clark (1946, p. 290) repeated the statement. However, the localities cited include " Aldinga lower beds ", now considered to be upper Eocene. Chapman and Cudmore (1934, Plate XII, Fig. 3) illustrated an undoubted *Stereocidaris* (with very reduced upper areoles) from these beds. But Fig. 4 of Plate XII, from the same beds, is apparently not a *Stereocidaris*, though assigned to *S. australiae*. H. L. Clark (1946, p. 290) suggested that it may be an undescribed *Stylocidaris* or a related genus. The other localities given by Chapman and Cudmore indicate that *Stereocidaris australiae* occurs in the Janjukian and in the Balcombian,

so that the total range in time of the species—or lineage—is very long, namely, from upper Eocene to middle Miocene. This may account for the considerable variation apparent in material of the species.

Phyllacanthus duncani Chapman and Cudmore (1934, pp. 131–133) is stated to range from upper Oligocene to lower Pliocene. The localities given indicate Janjukian to Kalimnan.

Prionocidaris scoparia C. & C., 1934, pp. 134–135. The localities given include the Aldingan lower beds (upper Eocene), the Waurn Ponds and Castle Cove (Janjukian), and Morgan (Balcombian), so the total range is also long—upper Eocene to middle Miocene.

Goniocidaris prunispinosa C. & C., 1928. The range is given (C. & C., 1934, pp. 135–137) as upper Oligocene to Miocene. Their localities include Aldinga lower beds, the Waurn Ponds, Aldingan, and Janjukian respectively, together with a number of localities which Dr J. Marwick (pers. comm.) says are Balcombian (Balcombe Bay, Grice's Creek, Altona Bay, Sorrento Bore, Gellibrand, Orphanage Hill, Murray Cliffs at Morgan, and Wongulla to Mannum). The range is therefore upper Eocene to middle Miocene.

Goniocidaris pentaspinosa C. & C., 1928. Stated (C. & C., 1934, p. 138) to range from upper Oligocene to Miocene. The localities given, however, suggest that the species is restricted to middle Miocene (Balcombian).

Goniocidaris murrayensis C. & C., 1934, pp. 138–139. Given as occurring also in Aldinga lower beds, so that the time range is from upper Eocene to middle Miocene (Aldingan to Balcombian).

Goniocidaris tubaria (Lamarck) and *G. mortenseni* C. & C., 1934, pp. 139–40. H. L. Clark (1946, p. 291) and Chapman and Cudmore (1934, pp. 139–40) have drawn attention to the similarity of *G. mortenseni* to the living species *G. tubaria*. The fossil form is known only from the upper Aldinga beds, of Kalimnan (lower Pliocene) age; but it probably belongs to the same lineage as the living species.

Chondrocidaris clarkii C. & C., 1934, pp. 141–142. The localities given would now be regarded as Janjukian to Balcombian, thus confirming the original time range given, upper Oligocene to middle Miocene.

Eucidaris sp. nov. Chapman and Cudmore (1934, p. 142, and Plate XIV, Figs 25, 26) describe and illustrate " club-shaped spines, *incertae sedis* " from various localities, stated to be Miocene. The illustrations, which unfortunately are not clear enough to determine all the characters, show a strong resemblance to the New Zealand *Eucidaris strobilata*, but they are of a distinct species, the spine having a much wider and more sharply truncated form in the Australian specimens; there is a strong suggestion of a terminal crown in the two spines to the left of the group numbered 25 in Plate XIV, and there is little doubt that the species should be referred to *Eucidaris*. The age is apparently Janjukian and Balcombian, upper Oligocene to middle Miocene.

In the Recent Cidarid fauna, Australia has species of *Eucidaris*, *Phyllacanthus*, *Goniocidaris*, *Histocidaris*, *Stylocidaris*, and *Prionocidaris* (including *Plococidaris*).

It is now apparent that the New Zealand Tertiary Cidarid fauna has its closest parallel in that of Australia. The generic content is essentially the same, and many of the species are closely related. Thus *Goniocidaris prunispinosa* of Australia matches *G. hebe* of New Zealand; *Goniocidaris pentaspinosa* matches *G. pusilla; Phyllacanthus duncani* is closely related to *P. wellmanae;* and similar species of *Eucidaris* occur in the middle Tertiary of both regions. Comparison of the two faunas is greatly hampered by two facts: one is that the New Zealand forms are known chiefly from the lower and middle Oligocene in stages not known to be represented in Australia; the other is that the facies of much of the New Zealand Miocene is unsuited to echinoid faunas, and relatively little is known of the New Zealand Miocene Cidarids as yet. It seems highly probable that they resembled those of the preceding Oligocene stages, and also those of the Australian Janjukian and Balcombian. Nearly all Australian Tertiary Cidarids so far discovered have come from south-eastern Australia and Tasmania. Little is known of their representatives in Western Australia. Australian Cidarid species seem to have longer time ranges than New Zealand ones. Possible reasons for the apparent

anomaly are: Firstly, Chapman and Cudmore accept rather broad specific diagnoses, and consequently include a wider range of forms in some of their species. Thus the material which they assign to *Stereocidaris australiae* (Duncan) seems to represent more than one species, and may possibly even include another genus, as Clark (1946) has remarked. Secondly, the scarcity of Miocene Cidarids in the material so far known from New Zealand may well mean that the ranges are still woefully incomplete.

FIJI

The Recent Cidaridae of Fiji and Tonga comprise only *Phyllacanthus imperialis*, *Eucidaris metularia*, and *Prionocidaris (Plococidaris) verticillata*. Hoffmeister (1932) found Eocene and Miocene limestones in Eua, Tonga, but these apparently did not yield any echinoid fossils. Ladd (1934) collected echinoids from the Suva Formation, in Viti Levu, and further Tertiary echinoids were collected by Ladd and Hoffmeister (1945) from limestones in the Lau Islands, between Viti Levu and Tonga. The echinoids of these collections have been described by Hawkins (1934) and H. L. Clark (1945). Using Clark's determinations, Johnson and Ferris (1950) have given some interesting faunal and floral lists showing the echinoids and molluscs associated with coralline algae in the Futuna and Fulanga limestones.

Hawkins (1934, p. 159) reported *Phyllacanthus* sp. indet. from the Suva Formation of Viti Levu. Mainly on foraminiferal evidence, this formation is correlated with the Miocene stages f and g, in the Van der Vlerk–Umbgrove classification of the Indonesian Tertiary (Ladd and Hoffmeister, 1945, p. 226 and Table 17). H. L. Clark (1945, pp. 312–315) reported *Eucidaris metularia*, *Phyllacanthus imperialis*, and *Chondrocidaris problepteryx*, all from the Futuna limestone of Lau. Ladd and Hoffmeister (1945) correlated the Futuna limestone with the Indonesian stage f, of lower Miocene age.

Eucidaris metularia and *Phyllacanthus imperialis* are also recorded by Ladd and Hoffmeister (1945, p. 268) from the Ndalithoni limestone of Lau, which they assign to either stage g or h of Indonesia, that is, to either the upper Miocene or to lower or middle Pliocene. From the Pleistocene Fulanga limestone an extinct species, *Phyllacanthus tylotus*, was described by H. L. Clark (1945, p. 313), and *Phyllacanthus imperialis* also was reported. To judge by Clark's figure (1945, Plate 41, d), *Phyllacanthus tylotus* looks more like a *Eucidaris*, but until a fuller description of the spine is available his determination must be accepted.

The most significant difference between the Tertiary and Recent Cidarid faunas of Fiji and those of Australia and New Zealand lies in the relative paucity of genera in Fiji, and especially in the absence of *Goniocidaris*. Despite the fact that the Malayan and Indonesian region is the richest in the world in species of the genus, *Goniocidaris* apparently failed to reach Fiji or Tonga, though it was well established in New Zealand and Australia from the Oligocene onwards. A well-known northern genus of the late Mesozoic and Eocene, *Stereocidaris*, had reached Australia and New Zealand by the beginning of the Oligocene, but seems never to have occurred at Fiji.

The Cidarids that now inhabit Fiji (and have done since the early Miocene) are of widespread Indo–Pacific distribution. They are species which have reached isolated outposts such as Mauritius and Tonga, and which apparently have the means of traversing deep-water gaps. It seems that during the Tertiary Fiji did not lie on the main migration route for shallow-water forms traversing the sea-beds between the northern Indian Ocean and Australasia; accordingly, its Cidarids are restricted. The uniformity of the Cidarid fauna since the early Miocene, and the long time range of the individual species, suggest a relatively stable, warm environment, similar to that of today. The fact that two important lineages have changed so little since the early Miocene implies a free intermingling with the rest of the Indo–Pacific stock of those two widespread species; that is, there has been no effective isolation of these two stocks. But the apparent absence of other genera occurring widely through the south-west Pacific (except Tonga) implies an effective isolation from New Zealand and Australia during the Tertiary.

There seems to be no other information on the Tertiary Cidaridae of the south Pacific, save for a record by Abrard (1946) of *Phyllacanthus imperialis* in the upper Tertiary of the New Hebrides.

Hawkins (1934, p. 161) saw in the echinoids from the Tertiary of Fiji some resemblance to those of the Northern Indian Gaj (Miocene) described by Duncan and Sladen. He also noted Indian Miocene elements in the New Zealand Tertiary echinoids, which he saw when the N.Z. Geological Survey collections were in London. Clark (1934) seems to have seen in the Fijian Tertiary echinoids only a generalized Indo–Pacific relationship, plus some endemism. Hawkins's views were not based on Cidaridae, and hence are better left for later discussion.

ANTARCTICA AND SOUTH AMERICA

H. L. Clark (1946, pp. 419, 492) has commented briefly on the New Zealand Recent echinoderm fauna in a summary which " reveals strikingly how different it is from that of Australia, and even from that of the East Indies. . . . The absence from New Zealand of numerous characteristic Australian genera . . . precludes any idea that New Zealand has derived any considerable part of its echinoderms from the island continent. On the other hand the notable proportion of its echinoderms derived from a southern source suggest a subantarctic or south temperate area with which New Zealand and possibly Tasmania and south-eastern Australia were associated . . . its (New Zealand's) echinoderms have very little significance as regards the composition and origin of the Australian fauna ".

These views, which are in direct opposition to those of Mortensen (1925, 1951) and Fell (1949a, b ; 1953), seem to stem from a number of misapprehensions. Clark disregarded the Australian echinoids in the existing New Zealand fauna, believing that their presence in New Zealand had not been proved. Fell (1949b), however, gave evidence that Australian species live on the northern coasts of New Zealand, and Mortensen (1943) had recorded a New Zealand echinoid from Tasmania. It is not possible to say on what Clark based the supposed southern or Subantarctic relationships, for he did not state his evidence. Only 2 per cent of existing echinoderm species of New Zealand are shared with South America, and half of them are cosmopolitan.

So far as the Cidaridae are concerned, the facts need merely be stated, without discussion. (1) There are no South American genera of Cidarids known from Australasia. (2) None of the eight Australian Cenozoic genera, and only one genus from New Zealand, is shared with Antarctica. (3) Of the six Antarctic and Subantarctic genera of Cidaridae, namely, *Aporocidaris*, *Ctenocidaris*, *Notocidaris*, *Homalocidaris*, *Rhynchocidaris*, and *Austrocidaris*, none is known from Australia, and only *Notocidaris* from New Zealand. The New Zealand record of *Notocidaris* (made in this bulletin) will require confirmation. The endemic New Zealand genus *Ogmocidaris*, however, may possibly be related to the southern *Austrocidaris*, and stem from Antarctic stock, but it is equally possible that *Ogmocidaris* arose from *Goniocidaris*.

Clark's views as to a relationship between New Zealand and some southern faunal area are therefore not supported by Cidarid evidence (nor by that of other echinoderm groups). As to the " absence from New Zealand of numerous characteristic Australian genera " (of which he lists twenty-one examples), the obvious reason for the absence is that the present waters of New Zealand are too cool to support these warm-water genera. Furthermore, the one Cidarid which he lists, namely, *Phyllacanthus*, was in fact present in the New Zealand fauna during mid-Tertiary times, when the climate was warmer. Dr Clark died in 1947 before his attention could be drawn to the fossil evidence from New Zealand; he would have been the first to acknowledge its significance.

WESTERN AMERICA

From the long stretch of coast between Ecuador and the south of Chile, including Peru, not one species of Cidarid is known as yet. From western Central America, including Ecuador, Galapagos, Panama, Mexico, and lower California, only a limited fauna is known. Ignoring the

valueless record of " *Cidaris* " from the Eocene and Oligocene, the only Tertiary Cidarids from this area are *Eucidaris* from the Miocene, Pliocene, and Pleistocene, and a very dubious record of *Hesperocidaris* from the Eocene of California (Grant and Hertlein, 1938). The Recent fauna of this long coast is likewise limited, including only *Eucidaris*, *Hesperocidaris*, and *Centrocidaris* (the two latter endemic). *Eucidaris* alone is shared with Australasia.

HAWAII

No Tertiary Cidaridae are known, because there are no Tertiary beds. The Recent genera are *Eucidaris*, *Histocidaris*, *Stereocidaris*, *Acanthocidaris*, *Prionocidaris*, and *Chondrocidaris*. The first three genera are shared with the New Zealand Cenozoic.

JAPAN

The Recent fauna includes a varied assemblage of species, referable to nine genera, of which five are represented in the New Zealand Cenozoic, namely, *Phyllacanthus*, *Histocidaris*, *Goniocidaris*, *Stereocidaris*, and *Eucidaris;* two more, *Prionocidaris* and *Stylocidaris*, are shared with Australia; whilst all nine genera are shared with Malaya and Indonesia.

MALAYA AND INDONESIA

Although this is today the richest area in the world for Cidaridae, little is known of its Tertiary forms. *Chondrocidaris* and *Phyllacanthus* occur in the Miocene. The Recent fauna includes every Australian genus, every Japanese genus, all the Indian Ocean genera except *Cidaris* and *Kionocidaris*, and all the genera of the New Zealand Cenozoic save *Notocidaris* and *Ogmocidaris*. On the other hand, none of the southern genera are represented, and only one of the west American.

INDIA

All the Australian Cenozoic Cidarid genera occur here, though *Goniocidaris* is not known later than the Pliocene. *Notocidaris* and *Ogmocidaris* are absent, but otherwise the New Zealand Cenozoic genera are represented, either by fossil or living species. *Cidaris*, an otherwise Atlantic genus, occurs at the Maldive Islands. *Phyllacanthus* was present in northern India in the Miocene, and *Chondrocidaris* is suggested by spines from the Pliocene of Mekran.

OTHER REGIONS

The Cidarid faunas of North Africa include *Histocidaris* in the Miocene and upper Tertiary; *Acanthocidaris*, *Stereocidaris*, and *Eucidaris* in the Recent; and *Phyllacanthus* and *Prionocidaris* from the Pliocene, Pleistocene, and Recent, in addition to early Tertiary species of " *Dorocidaris* " and " *Leiocidaris* ". The relationships are chiefly with the Indian Ocean faunas, but the two latter fossil " genera " probably include forms with European affinities.

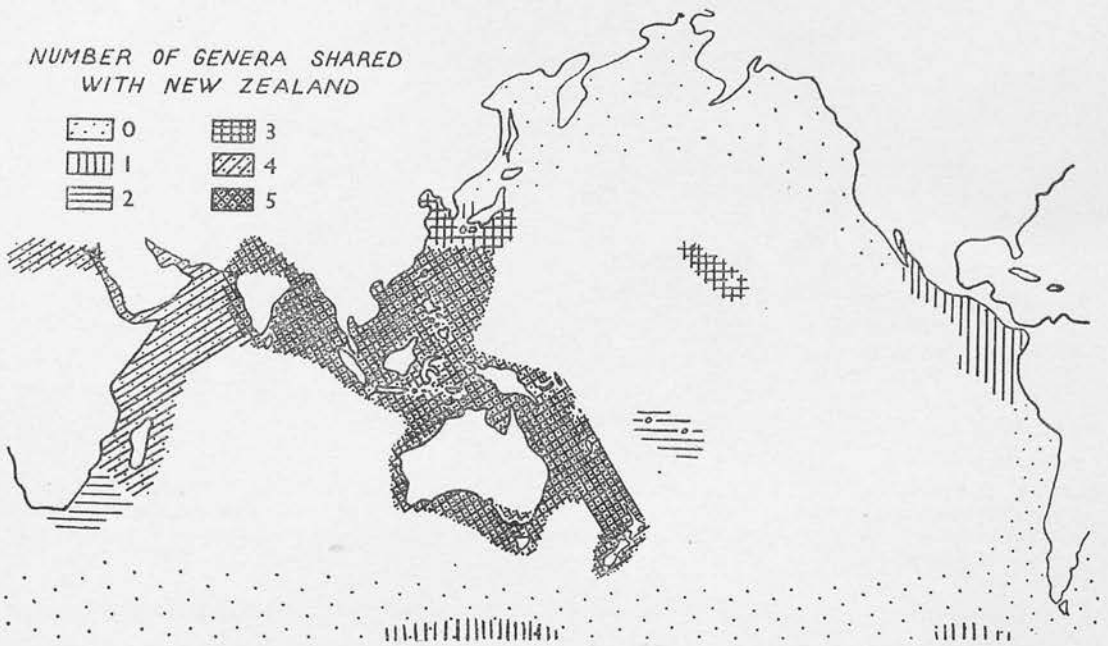
East Africa, including Madagascar, possesses *Stereocidaris*, *Goniocidaris*, *Prionocidaris*, and *Eucidaris* in the existing fauna, whilst *Chondrocidaris* is restricted to the Miocene, and *Phyllacanthus* ranges from the Miocene to the Recent.

South Africa possesses *Stereocidaris*, possibly *Goniocidaris*, and the endemic genus *Kionocidaris*, all in the existing fauna. The single Tertiary " *Cidaris* " is of uncertain relationship.

The only other region with any significant resemblance to the Indo–Pacific in its Cidaridae is Europe. Although the Cretaceous and Eocene faunas contained genera such as *Stereocidaris* and *Prionocidaris*, most of the European Tertiary Cidaridae were members of various northern fossil groups such as *Rhabdocidaris*, *Plegiocidaris*, *Cyathocidaris*, and *Dorocidaris*, whose relationship to Indo–Pacific genera is by no means clear, but cannot be close.

ORIGIN AND MIGRATION ROUTES

The faunal relationships outlined in the previous chapter may now be condensed and expressed graphically in the form of a map (Text fig. 1) which shows the distribution over the Indo–Pacific of regions possessing none, one, two, three, four, or five of the recorded New Zealand Cenozoic genera. A genus is regarded as present if it is recorded at any time from Oligocene to Recent. In this manner some idea is obtainable of the broad relationships, and therefore origin, of the New Zealand Cidarid fauna of the whole Cenozoic. Clearly the relationship is mainly with the Indo–West-Pacific, of which the New Zealand region forms the south-eastern limit. Most of the New Zealand Tertiary Cidarid fauna must have originated somewhere within the central double-hatched area, which includes northern India, Malaya, southern Japan, Indonesia, and Australasia. But where?

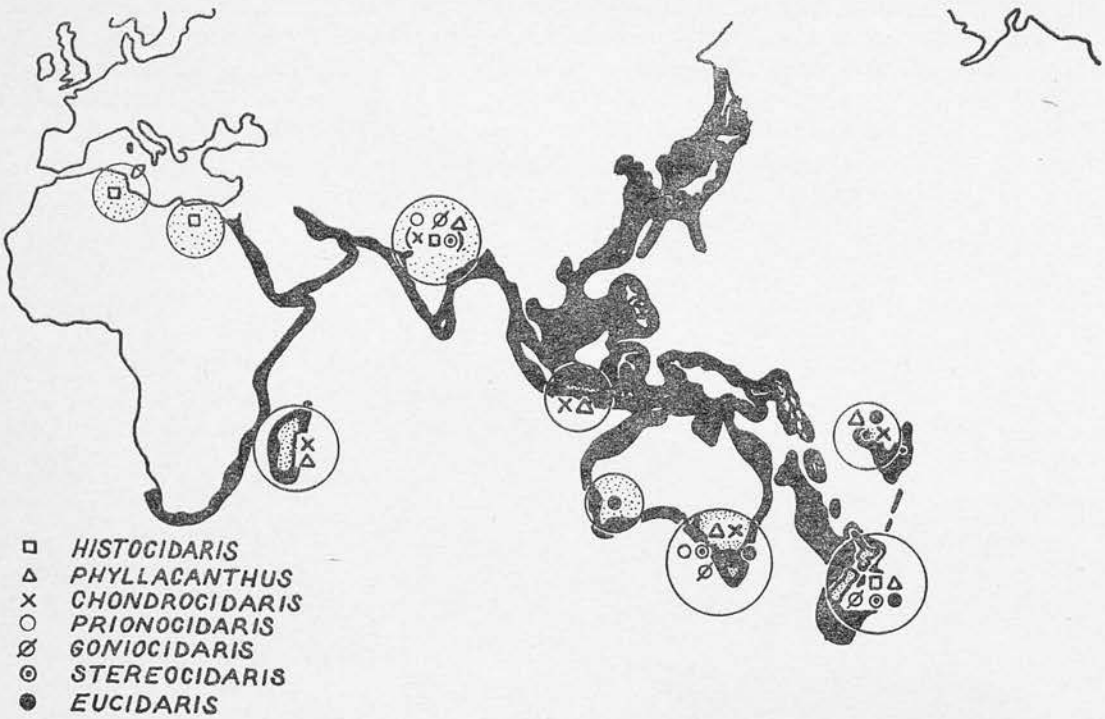


TEXT FIG. 1. Tertiary and Recent distribution of genera of Cidaridae in the Indo–Pacific, showing the number shared with New Zealand

To answer this would require more exact knowledge than is available of the distribution of the genera throughout the Tertiary. At present the only genus of the six for which there is anything approaching the required amount of data is *Goniocidaris*. However, some gaps in our knowledge of past Tertiary distribution of Cidarids can be sketched in by inferences drawn from other data. Accordingly, the probable distribution of some Indo–West-Pacific Cidarid genera during the middle Tertiary has been indicated in Text fig. 2.

There is direct evidence that by Miocene times *Goniocidaris*, *Prionocidaris*, and *Phyllacanthus* were present in northern India. Furthermore, *Stereocidaris* and *Prionocidaris* had been established in Europe during the Cretaceous and Eocene, and both genera had reached Australasia by the late Eocene. It is therefore extremely probable that *Stereocidaris* also was present in northern Indian seas during the Eocene, or earlier. It is also known that *Chondrocidaris* was present in Australia, in Java, and in Madagascar during the Miocene. Therefore it is highly probable that it was also present in India, which lies on the shallow-water belt between these extremes; indeed, certain Miocene spines from India recall *Chondrocidaris*. *Histocidaris* was apparently present in northern Africa in the Miocene, and already present in New Zealand in the Oligocene. The genus had

probably therefore already achieved its present widespread distribution by Miocene times. It may be concluded, therefore, that the northern Indo–Pacific region in the Miocene was inhabited by *Goniocidaris*, *Phyllacanthus*, *Chondrocidaris*, *Histocidaris*, *Stereocidaris*, and *Prionocidaris*, and that some



TEXT FIG. 2. Probable distribution of seven genera of Cidaridae during the middle Tertiary. Three of the northern Indian plots are inferred only, and are shown in brackets. A possible former shallow-water migration path is suggested by the areas filled in black; these are parts of the sea floor which at present lie above the minus 2,000-metre contour line

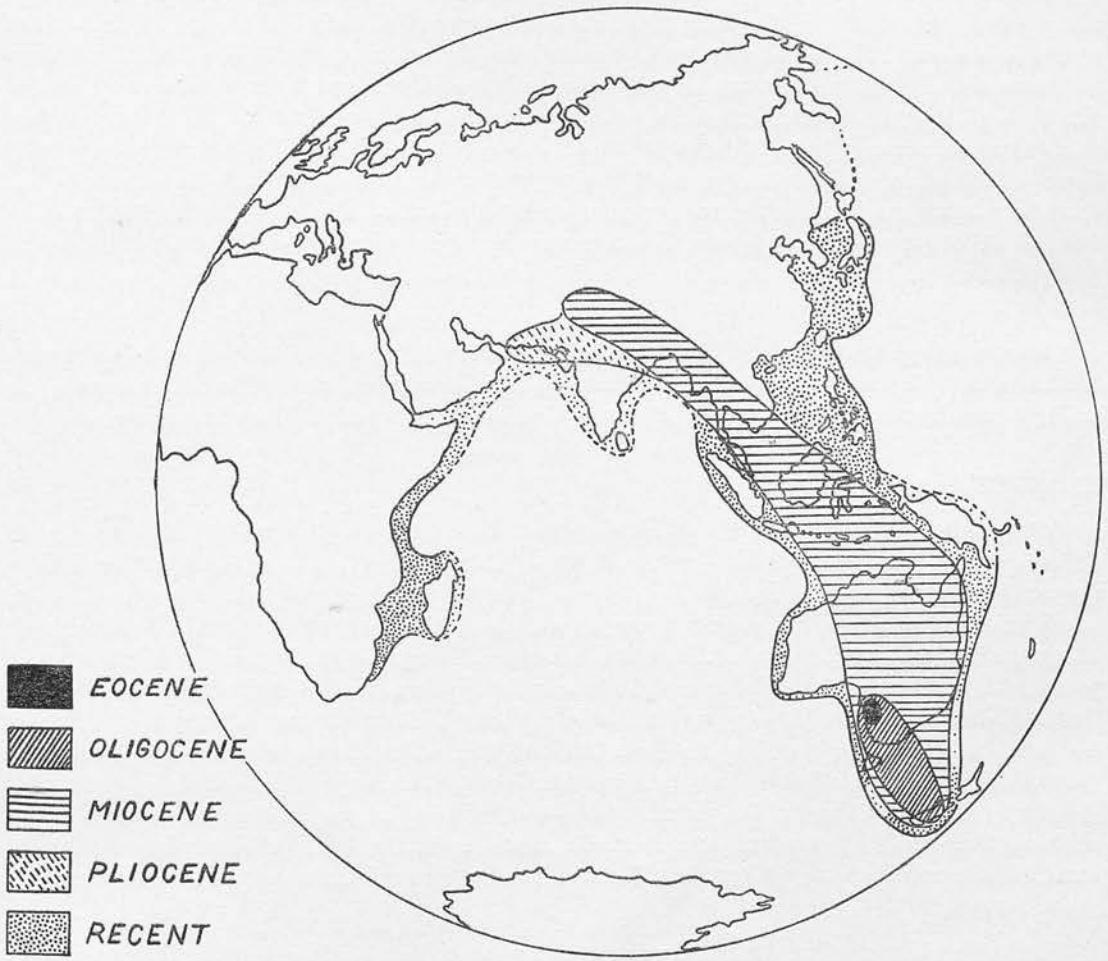
of these genera (but not, apparently, *Goniocidaris*) had probably been present since Eocene times or earlier. Thus, if the distribution of the six genera during the Oligocene and Miocene is plotted, they are seen to form an axis stretching from northern India to Australasia. This probably constitutes the actual migration route; for *Phyllacanthus* and *Chondrocidaris* were certainly present in Java, midway along the route, during this interval. To the east, *Eucidaris* and *Phyllacanthus*, perhaps also *Chondrocidaris*, had colonized Fiji.

The direction of migration along the Malayan–Indonesian arc was probably from north to south in the main. *Stereocidaris* had Mesozoic northern ancestors, and *Prionocidaris* was a European genus during the Cretaceous and Eocene. These genera evidently moved south-eastward into the Indo–Pacific, and thence presumably to Australasia. *Histocidaris* may have crossed through deep water, but most genera would follow the shallow-water route of the continental shelf and its neighbourhood. *Goniocidaris*, however, may well have moved in the reverse direction, that is, from Australasia north-westward to India. The case is an interesting one, and warrants separate discussion.

The oldest known Goniocidarids are *G. spinosa* and *G. murrayensis* from the lower Aldinga beds (upper Eocene) of South Australia.* *Goniocidaris hebe*, an undoubted member of the genus, occurs in the lower Oligocene of New Zealand. Thus, by the early Oligocene the genus was well established in Australasia, though unknown from other parts of the world. The approximate limits of

* Records of *Goniocidaris* from the Cretaceous of Europe, Eocene of Jamaica, and Miocene of Patagonia have been shown to be erroneous by Mortensen (1928).

distribution for four successive intervals during the Cenozoic are plotted in Text fig. 3. The early Oligocene distribution is restricted to Australasia. By the Miocene the genus was also represented by two species in northern India (Gaj). In the Pliocene it extended to the Persian Gulf, where spines similar to Recent Goniocidarids occur in the Mekran Series. It was still represented in south-east Australia, and may well have been present in New Zealand, though Pliocene fossils are not yet known. The Recent distribution extends still further, to include southern Japan, East Africa (the single species *G. indica*), probably South Africa (a broken test of *Goniocidaris* is known from Natal), as well as the Australian region, and Malaya–Indonesia (the present centre of distribution of the genus). There would seem on the face of it to be some evidence of an Australasian origin



TEXT FIG. 3. Approximate limits of distribution of *Goniocidaris* at successive intervals during the Cenozoic

for *Goniocidaris*—perhaps from *Stereocidaris* ancestry during the Eocene—followed by subsequent migration northward in the late Oligocene or early Miocene, eventually leading to the colonization of the east coast of Africa and of Japan.

Lastly, we may consider the distribution of the Cidarid genera which have had a more or less widespread range in the Indo–Pacific since the Pliocene (ignoring, that is, the purely local endemic genera *Ogmocidaris*, *Kionocidaris*, *Centrocidaris*, *Hesperocidaris*, and *Actinocidaris*). Australia remained relatively rich in genera, with *Phyllacanthus*, *Stylocidaris*, *Prionocidaris*, *Goniocidaris*, *Eucidaris*, and *Histocidaris*. On the other hand, New Zealand lost most of the middle-Tertiary genera, retaining

only *Stereocidaris* (or some related genus) in the Pliocene, and *Goniocidaris*, which survives into the Recent fauna with one endemic species. Over the rest of the Indo–West-Pacific the Cidarids survive in great force, save only in South Africa, where, indeed, they seem never to have been abundant. In Malaya and Indonesia they reach a peak, with twelve genera and numerous species. In southern Japan also the group is well represented by some nine genera. Thus the one surviving New Zealand species of *Goniocidaris* is the last remnant of the old Indo–Pacific Cidarid fauna which once inhabited New Zealand seas. The fauna has been so depleted that it is scarcely possible to perceive its origin merely by considering the Recent representatives.

Moreover, not only has the old Indo–Pacific element been reduced to a bare vestige, but the aspect of the existing fauna is further modified by a hint of isolation. An endemic genus, *Ogmocidaris*, has appeared, taking the place of the vanished elements of the mid-Tertiary. The origin of *Ogmocidaris* is uncertain, but it may be related to *Goniocidaris* or to *Austrocidaris*. The second alternative would not necessarily mean that *Ogmocidaris* is a southern entrant into the fauna. *Austrocidaris*, in addition to its southern species, has also deep-sea Pacific species. *Ogmocidaris* is a deeper-water form, known only from off the east coast of the North Island of New Zealand at depths ranging down to 200 fathoms. It is absent from the upper part of the continental shelf. It is thus possible that the genus has arisen from some deeper-water Austrocidarid. *Goniocidaris umbraculum*, ranging from Cook Strait to Stewart Island, has the more southern distribution. If the Nukumaruan (middle Pliocene) Cidarid referred in this bulletin to *Notocidaris* is correctly placed, it must have been an immigrant from the south.

Summarizing, the conclusion is reached that the New Zealand Cidarid fauna, like that of Australia, is derived from early Tertiary Indo–Pacific faunas, but, unlike that of Australia, has suffered great depletion during the late Tertiary, and has further evolved an endemic genus.

ENDEMISM AND ISOLATION

One of the Recent genera and all Tertiary and Recent species of New Zealand Cidarids are believed to be endemic. With fuller knowledge of Australasian faunas, this rather remarkable degree of endemism may be found to be illusory. But it is unlikely that the endemism will fall to much below 80 per cent (the present figure for whole Recent echinoderm fauna). Echinoids, on account of their different habits and habitats, lack some of the means of distribution which are open to asteroids and ophiuroids—such as epiplanktonic distribution on kelp—and so tend to reflect this fact in higher endemism. It is apparent that in the later Tertiary (at least) a very high degree of isolation has been experienced by the New Zealand echinoderm fauna as a whole. Even in the case of ophiuroids the endemism is very high. Similar isolation may also have affected the middle Tertiary echinoderm faunas, for, despite the close similarity in generic content of the Tertiary echinoid faunas of New Zealand and Australia, and despite the fact that Australian species can sometimes be matched by similar New Zealand species, nevertheless the two faunas seem to be quite distinct.

Assuming that the foregoing theory as to the common origin of the two Australasian faunas is approximately correct, one might add this further deduction: New Zealand did not receive its echinoid fauna by way of Australia, but rather received it independently from some common point on the northern migration route. Perhaps the forking of the two paths would occur off northern Queensland (see Text fig. 2), the New Zealand immigrants following the Lord Howe Rise, or some equivalent Tertiary ridge. A reverse migration from New Zealand northward, and so into Australia, may have become difficult for echinoid lineages once they had become adapted to the cool Pliocene waters in New Zealand. Even in the earlier middle Tertiary times, despite the probability that New Zealand waters were tropical or sub-tropical, there may have been a temperature gradient sufficiently marked to prevent migration from New Zealand to Australia via the shallow, but presumably warmer, northern route.

Whatever may have been the case, it is reasonable—indeed, in the case of echinoids, it is probably essential—to infer that New Zealand has been, and continues to be, an area which has received echinoderm immigrants from the subtropical north-west Tasman, and probably in former times from the Coral Sea also. But New Zealand has not sent back emigrants in the reverse direction. Larval dispersal by way of the East Australian Current, and dispersal by epiplanktonic drift, would likewise necessarily be a one-way process, with north-east Australia as the donor, and New Zealand as the recipient. Once lineages have entered our seas, they have been cut off from their parent stocks, and have accordingly undergone geographic speciation. Thus, on a species basis, the endemism becomes pronounced, but on a generic basis the Indo–Pacific and Australian relationships remain clearly perceptible. In the same way, New Zealand would tend to have a donor relationship to South America, through the medium of the west-wind drift. But the great expanse of deep water between New Zealand and South America would make such dispersal exceedingly rare and precarious. Cidarids seem never to have crossed the gulf. One echinoid, *Pseudechinus*, and starfish such as *Asterodon*, have a strong development in New Zealand, and a weak extension to South America; they may be examples of echinoderms which succeeded in crossing the South Pacific Ocean. This topic, as also the relative importance in the dispersal of echinoderms of shallow-water sea-floor migration on the one hand, and of surface drift on the other, has been discussed recently elsewhere (Fell, 1953) and further elaboration here is unnecessary.

THE TERTIARY CLIMATES OF AUSTRALASIA

THE EVIDENCE OF THE *PHYLLACANTHUS–EUCIDARIS* FAUNA

On evidence drawn from groups other than echinoderms, chiefly Mollusca and Foraminifera, Fleming (1949) has suggested that in New Zealand the Eocene may have been warm-temperate, the Oligocene a little cooler, and the Miocene tropical, with cooling towards the onset of the Pliocene. With most of these conclusions the evidence provided by New Zealand Tertiary echinoids is not inconsistent. The presence of *Phyllacanthus* in the Waiauan and Kapitean indicates warm Miocene conditions. The notable absence from New Zealand of warm-water echinoids such as *Schizaster* after the Miocene, and the incursion of cool temperate forms in the Pliocene, support Fleming's conclusions, as briefly mentioned elsewhere (Fell, 1953). There is, however, some discrepancy so far as the Oligocene is concerned. The relatively rich assemblage of Cidarids must be taken into account when New Zealand Oligocene climates are under discussion; for, not only does the assemblage include some genera whose determination seems beyond all reasonable doubt to be reliable, but also two of these genera occur today only within well-marked climatic zones. The Cidarids seem to point strongly to tropical or sub-tropical climates in New Zealand during the early and middle Oligocene. The Cidarid evidence, since it is independent, warrants detailed treatment.

Three genera which do not offer any conclusive information may be briefly noted first. *Histocidaris* is mainly a deeper-water genus with only a few littoral species, so that its bearing on littoral temperatures is by no means clear. It should, however, be noted that the majority of living species occur in the tropics, and the remainder are sub-tropical. The two fossil species so far referred to the genus (Lambert 1931, 1932) both come from an area likely to have been warm, namely, from Algiers (upper Tertiary) and Egypt (Miocene). The large size of the Waihao *Histocidaris mckayi* also suggests a warm habitat.

Goniocidaris and *Stereocidaris* likewise provide no clear evidence either way. Their Recent species occur in tropical, in sub-tropical, and in temperate waters. The former genus enters the cool-temperate Sagami Sea, and still cooler waters in Foveaux Strait, 46° 45′ S., where winter surface-water temperatures average *ca.* 8° c. However, the evident relationship between the New Zealand

lower and middle Oligocene species and the Australian mid-Tertiary forms does seem to imply similar environmental conditions during the deposition of the New Zealand Landon Series on the one hand, and the Australian Janjukian on the other.

Eucidaris comprises five Recent species; all are littoral forms, occasionally found beyond the continental shelf. *E. australiae* is known only from the type locality, off Albany, Western Australia, 35° S. (Mortensen, 1950). *E. clavata* is apparently restricted to Ascension, 8° S., and to Saint Helena, 17° S., both in the tropical mid-Atlantic. Specimens in the Paris Museum, supposedly from Magellan Strait, are, according to Mortensen (1928), almost certainly wrongly labelled. *E. tribuloides* is a widely ranging Atlantic species. On the western coasts its northern limit is South Carolina, *ca* 33° N., and its southern limit is near Bahia, 12° S. On the eastern side of the Atlantic it ranges as far north as the Azores, 39° N., and the Moroccan coast, whilst its southern limit is uncertain. It is known that it occurs as far south as the Gulf of Guinea, and a form at Loango, 4° 35′ S., is probably this species. *E. thouarsii* is the west-American form, ranging from the Gulf of California, *ca* 23° N., southward to the equator, at the Galapagos Islands and Ecuador (H. L. Clark, 1948). *E. metularia* is the wide-ranging Indo–West-Pacific species; its north-western limit lies in the Gulf of Suez, 29° N., its south-western limit at Mozambique, 15° S. The north-eastern limit is at Oshima, in the Ryukyu Islands, 29° N., and the south-eastern limit seems to be Fiji, *ca* 18° S. In Australia it does not seem to range south of Flinders Banks (northern Australia).

Authoritative information on the distribution of *Phyllacanthus* is given by H. L. Clark (1946), who has had extensive experience in Australia, the main home of the genus. All species are littoral reef-dwellers. *Phyllacanthus imperialis*, the only widely ranging species, extends from the Gulf of Suez, in the north-west, and Oshima, in the north-east, both in 29° N. latitude, southward to Tonga, 18° S., in the east, and to Madagascar, *ca* 23° S., in the west. Its total range is thus similar to that of *Eucidaris metularia*. In Australia, *P. imperialis* seems to occur only in the Torres Strait region, but it is possible that the species intergrades with *E. parvispinus*. The latter species ranges up the eastern Australian coast from 37° S. to an unknown distance north, and also occurs at the Kermadec Islands, 31° S. A record of the species at Tasmania has not been authenticated. *P. longispinus* is restricted to tropical north-west Australia. *P. magnificus* occurs in sub-tropical west Australian waters, between 28° and 32° S. *P. irregularis*, the south-western and southern species of Australia, occurs between 32° and 35° S. *P. dubia*, the only species of *Phyllacanthus* which does not occur in Australia, is known solely from its type locality, the Bonin Islands, 27° N.

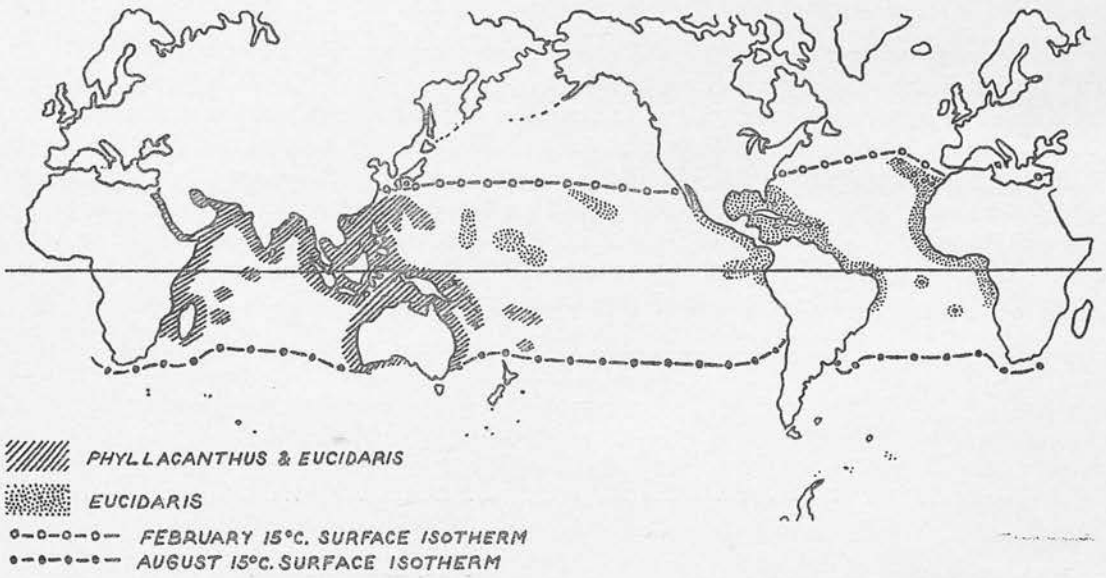
When the distributional data for *Eucidaris* and *Phyllacanthus* are plotted on a map (Text fig. 4) it is easier to assess the distribution pattern in terms of other factors. *Eucidaris* is seen to occupy a belt of warm waters encircling the globe, roughly corresponding to the geographical tropics, though transgressing the tropics in certain more or less well-defined areas. The northern limit of *Eucidaris* extends from Suez, round the southern shores of Asia to the Ryukyus, across the Pacific to southern California, from South Carolina north-eastward to the Azores, then south-eastward to Morocco. The southern limit runs from the African coast at Mozambique, south-eastward to south-west Australia, thence to Fiji, and across the Pacific to Galapagos and Ecuador, from Bahia in Brazil to central west Africa. *Phyllacanthus* occupies the Indo–West-Pacific quadrant of the range of *Eucidaris*, but extends also further along the south-west coast of Australia, and from New South Wales to the Kermadecs, Fiji, and Tonga.

Reference to Sverdrup, Johnson, and Fleming (1942, Chart VI) shows that both genera encounter summer salinities in the Red Sea of over 40 p.p. mille, and both likewise encounter salinities as low as 33–34 p.p. mille in Indonesia. *Eucidaris* also meets low salinities in the Central American region, and widely varying salinities on the Brazilian and west African coasts. Salinity is therefore not a significant factor in the distribution pattern of *Phyllacanthus* and *Eucidaris*.

On the other hand, study of the surface temperature charts of the oceans (Sverdrup, Johnson, and Fleming, 1942, Charts II and III), suggests that temperature may well be a determining factor. In the map showing the distribution of the two genera (Fig. 4), the winter surface isotherms for

15° c., i.e., the February isotherm for the northern oceans, and the August isotherm for the southern oceans, have been inserted for comparison. The similarity of the isotherm patterns and the distributional limits is quite striking in the northern Pacific, the southern Indian Ocean, and, especially, the northern Atlantic. The correspondence is less marked in the southern Atlantic and Pacific; but this discrepancy may be partly explained by the cold Humboldt Current, which may have introduced cooler southern competitive echinoids into the Chilian coastal fauna; also, the echinoid faunas of the few islets in the southern Pacific have not been investigated, and *Eucidaris* may well occur farther south than is yet known.

In any case, on the existing evidence, it is apparent that neither *Phyllacanthus* nor *Eucidaris* occurs in seas whose surface waters fall below about 15° c. during the cool months; hence the presence of *Phyllacanthus* along the southern coast of western and eastern Australia, and at the Kermadecs. Unpublished data assembled by the Oceanographic Observatory, Wellington, indicate that the northern waters of New Zealand lie within the 15° c. winter isotherm, so *Phyllacanthus* may yet be found living on the Northland peninsula.



TEXT FIG. 4. Recent distribution of *Phyllacanthus* and *Eucidaris*, showing the possible value of these genera as temperature indicators in paleoecology

The distribution of fossil species of *Phyllacanthus* and *Eucidaris* has been discussed by Mortensen (1928) and also elsewhere in this work (pp. 11–14), and it need only be stated here that all known fossil species were apparently members of warm-water faunas.

One other point may be noted: it seems to be a general rule that echinoids with very massive primary radioles, like those of the New Zealand Oligocene *Eucidaris coralloides*, *E. strobilata*, and *Phyllacanthus titan*—compare *Heterocentrotus* and *Chondrocidaris*—are not known from existing cool or cold waters, nor are their fossil remains known to be associated with any former cool-water fossil assemblage. It is true that the antarctic species *Notocidaris remigera* has large, flattened spines (Mortensen, 1950), but these—as Mortensen stresses—are so delicate that they break on handling, and are not really comparable with those of the type under discussion.

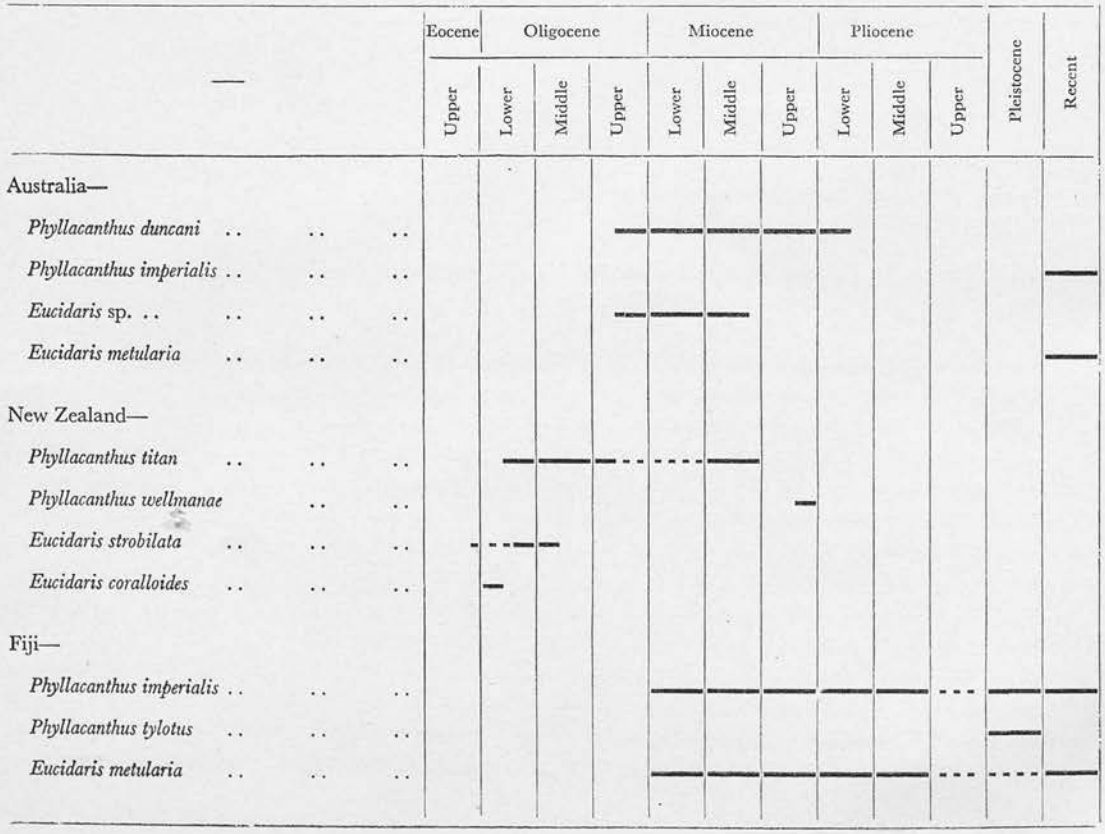
It is concluded, therefore, on the Cidarid evidence from the New Zealand Tertiary, that in early and middle Oligocene times the whole New Zealand area probably lay within sub-tropical waters, and that, if seasonal differences then existed, the winter 15° c. surface-water isotherm lay some six or eight hundred miles south of its present position. The climate of south Canterbury,

where the remains of large Oligocene echinoids now occur, would then have been at least as warm as that of the Kermadec Islands at the present day, or alternatively, if the land temperatures were lower, then a warm current maintained a southern extension of sub-tropical waters into south Canterbury latitudes. How long these conditions lasted cannot be determined from our present knowledge of the fossil Cidarids, but the presence of *Phyllacanthus* in the Waiauan and Kapitean stages, and other echinoid evidence, together with that provided by Mollusca and Foraminifera, suggest that warm conditions persisted through most of the Miocene—as Fleming (1949) has already deduced. The only real point of difference concerns the time at which warm conditions began—and Cidarid evidence favours the early, rather than late, Oligocene. Any other conclusions would imply an extraordinary difference in the habit of Tertiary Cidaridae compared with their Recent representatives—an implication which is unacceptable until more detailed evidence is presented to justify inferring a cool Oligocene climate in the New Zealand area. It would also lead to the puzzling inconsistency that Australian Janjukian–Balcombian Cidarid faunas, regarded as part of a warm Indo–Pacific element in the Australian mid-Tertiary, comprised a faunal assemblage extremely similar to those of a supposed cool New Zealand Oligocene.

THE TERTIARY CLIMATES OF NEW ZEALAND, AUSTRALIA, AND FIJI

Although the foregoing argument is only a tentative approach, requiring confirmation, it is of some interest to see what are its other implications. There are three land areas in the south-west Pacific where something is now known of the history of *Phyllacanthus* and *Eucidaris* during the Tertiary; all three are believed to be continental in structure. These are the present eastern margin of Australia, and the islands of Fiji and New Zealand. Text fig. 5 shows the known time ranges of the two genera in each of these areas. The correlation used is that indicated on p. 23.

TEXT FIG. 5. *Known Time Ranges of* Phyllacanthus *and* Eucidaris *in Australia, New Zealand, and Fiji*



In eastern Australia both genera are represented in the Tertiary from the Janjukian to the Balcombian; after that, *Phyllacanthus* continues to the Kalimnan. Both are represented in the Recent fauna. In New Zealand both genera were present in the Oligocene, and *Phyllacanthus* persisted until the end of the Miocene. In the Pliocene calcareous facies there are cool-water echinoids, including a cidarid. Neither *Phyllacanthus* nor *Eucidaris* is known to occur, and neither genus is represented in the existing fauna. In Fiji, ignoring a brief hiatus (probably reflecting incomplete collecting through lack of exposed beds), both genera follow an unbroken course from early Miocene times down to the present day.

These facts seem to imply that Fiji has enjoyed a warm climate continuously from the early Miocene onwards. New Zealand would also be warm in the middle Tertiary, from the early Oligocene on, but at some time between the Kapitean (upper Miocene) and the Waitotaran (early Pliocene) the climate became cooler, and it has remained too cool for *Phyllacanthus* and *Eucidaris* ever since. In eastern Australia the gap between the middle and upper Tertiary records and the Recent species is somewhat equivocal. It might mean that conditions were never cooler than they are now, during the interval between the late Oligocene and the Recent; in such case, then, the hiatus in the sequence merely reflects incomplete collecting. Or it might mean that a comparatively brief period of cooler climates intervened between the early Pliocene and the Pleistocene, and that species of both genera, after a temporary northward retreat, have re-established themselves in the Recent fauna. From other evidence, the latter alternative would seem more probable.

CORRELATION OF NEW ZEALAND AND OVERSEAS STAGES

The standard divisions of the New Zealand Upper Cretaceous and Tertiary (Finlay and Marwick, 1947) are shown in Text fig. 6, on following page. Finlay (1947) proposed the following correlation with Australia and other overseas regions, based on the evidence of Foraminifera:

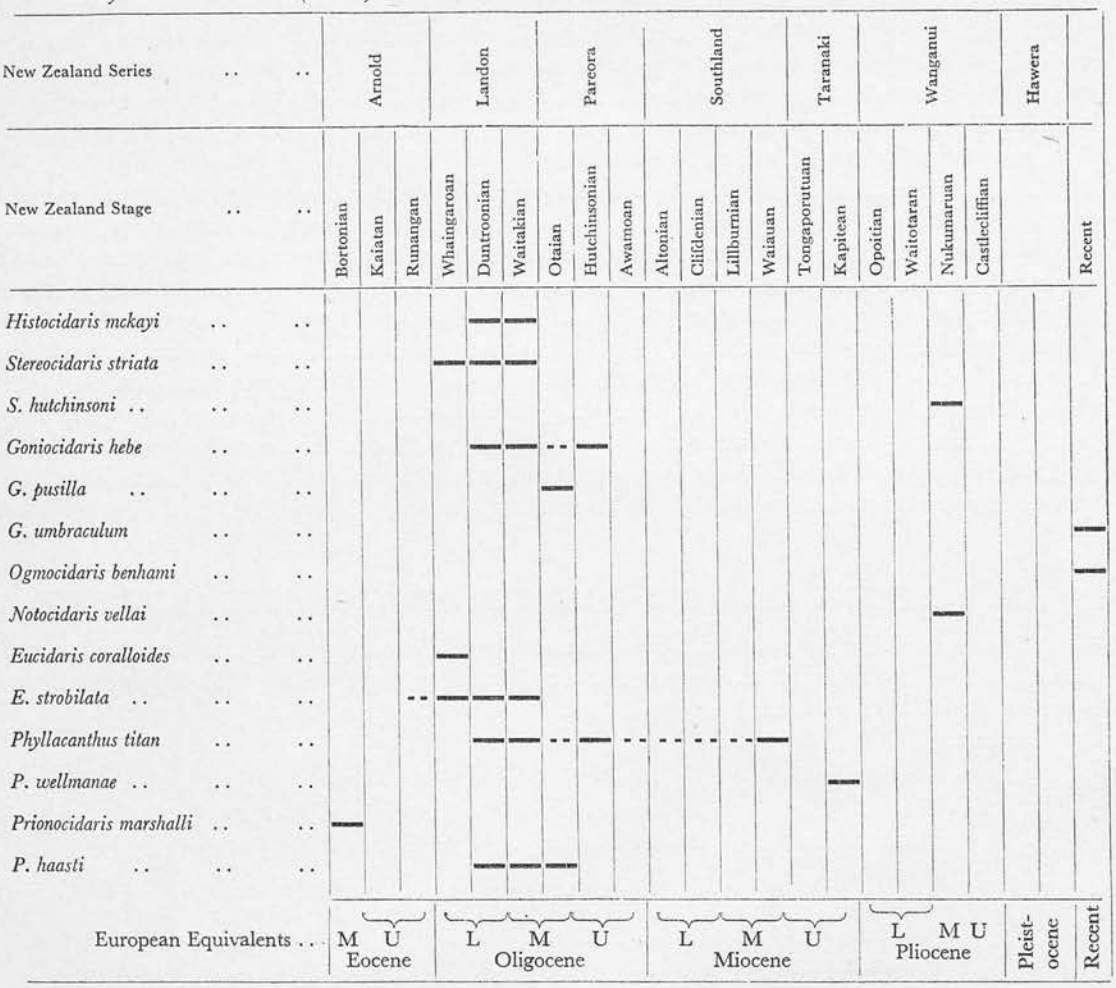
New Zealand	Australia	Europe
Castlecliffian	Werrikooian	Upper Pliocene
Nukumaruan	Adelaidean	Middle Pliocene
Waitotaran, Opoitian	Kalimnan	Lower Pliocene
Kapitean	Mitchellian	Uppermost Miocene
Waiauan, Lillburnian, Clifdenian	Balcombian	Middle Miocene
Altonian	Janjukian	Lowermost Miocene
Kaiatan	Giralian	Upper Eocene

On this basis the interval between the Giralian and the Janjukian, corresponding to the whole of the Oligocene and to the interval Whaingaroan–Awamoan in New Zealand, is lacking from the Australian column.

When the time ranges of the Australian Cidaridae are expressed in terms of Finlay's table, the species *Stereocidaris australiae*, *Goniocidaris prunispinosa*, *G. murrayensis*, and *Prionocidaris scoparia* have rather protracted time ranges from upper Eocene to middle Miocene (Giralian to Balcombian). Even allowing for the possibility that Chapman and Cudmore (1934) have made single species out of continuous lineages of related forms, the long ranges with so little change seem surprising, the more so since the genera concerned exhibit great diversity of form in the Recent Indo–Pacific.

The New Zealand Landon and Pareora series contain a Cidarid fauna which has its closest counterpart in Australia. *Goniocidaris hebe* parallels *G. prunispinosa*, *G. pusilla* closely parallels *G. pentaspinosa*, *Prionocidaris haasti* may represent *P. scoparia*, and other genera have representatives on either side of the Tasman.

TEXT FIG. 6. *Known Time Ranges of New Zealand Cenozoic Cidaridae. The Divisions of the New Zealand Tertiary, and Their Correlation with Those of Europe, are those Proposed by Finlay and Marwick (1947)*



When the time ranges are compared, on Finlay's correlation, these New Zealand forms straddle that part of the Australian ranges which is supposed to be represented by a break in the column—the Oligocene interval. On the surface it might seem that the correlation is faulty, and that the New Zealand Landon and Pareora series correspond to the Janjukian and Balcombian of Australia. In this way the long Australian time ranges could be reduced, and the two trans-Tasman faunas given a roughly contemporary range. Such a drastic alteration, however, does not seem to be the real way out of the difficulty; certainly it could not be justified on echinoid evidence. One great defect in our data is our present lack of information on the Cidaridae of the Southland Series in New Zealand. When they are eventually discovered it may very well turn out that they will prove to be merely extensions of the lineages already known from the Pareora Series.

A recent discovery makes this the more probable, for in 1953 *Phyllacanthus wellmanae* was found in the Taranaki Series (Kapitean Stage). This species is closely related to the Australian *Phyllacanthus duncani*, which occurs in the Janjukian, Balcombian, and Kalimnan. Thus it would now appear that it is only those Australian species which range *below* the Janjukian that have counterparts in the New Zealand Landon and Pareora series, whilst the one Australian species that has a counterpart in the New Zealand Miocene is known only from the Janjukian *onwards*. This

new discovery makes it seem quite probable that the New Zealand Southland Series will eventually yield a Cidarid assemblage comparable with that which accompanies *Phyllcanthus duncani* in Australian formations of Janjukian to Kalimnan age. That the New Zealand Pliocene stages corresponding to the Kalimnan are known to contain a different echinoid fauna is merely indicative of the change of climate at the close of the Taranaki Series, the Australian seas retaining the warm-water assemblage after New Zealand contemporary seas had lost it. The Cidarid evidence, therefore, does not throw doubt on the validity of Finlay's trans-Tasman Tertiary correlation.

An added reason for caution is the apparent stability of Cidarid species in Fiji over the whole interval between the Suva and Futuna formations (lower and middle Miocene) and the Recent. It is possible that speciation of Cidaridae in Australasia was very limited during the warm middle Tertiary, and only became pronounced with the disturbed climatic conditions which are believed to have set in at the end of the Miocene.

It should be noted, however, that a preliminary examination of the rest of the New Zealand Tertiary echinoids has suggested some rather close parallels between the Duntroonian–Waitakian faunas on the one hand and the Janjukian on the other. A case in point is that of *Brochopleurus australiae*, which is apparently represented in both faunas.

Although the Australasian Cenozoic Cidaridae comprise a relatively rich assemblage in comparison with that of any other region, nevertheless the actual number of species is small. Therefore their stratigraphic relationship, together with that of the other echinoids, is better left for discussion in subsequent parts of this work. Meantime a preliminary account of the echinoid succession is available elsewhere (Fell, 1953). Text fig. 6 indicates the known time ranges of the New Zealand Cidarids.

SYSTEMATICS

In the final volume of his *Monograph of the Echinoidea*, Mortensen (1951) summarized his views on the evolution of the echinoids, and proposed a classification which will be followed throughout this work. The major groups, and their key features, are given below.

Class ECHINOIDEA

Compact unstalked echinoderms, without arms, having a complex shell made up of interlocked ambulacral and interambulacral plates which bear movable spines.

Sub-class REGULARIA

Mouth centrally placed on the lower surface, anus centrally placed above.
Five orders are represented in the New Zealand Cenozoic:

Order CIDAROIDA.—Test globe-shaped; interambulacral plates each with one large boss, carrying one large radiole; gills absent; teeth not keeled, epiphyses of jaws not meeting above pyramid; primary radioles with a cortex.

Order LEPIDOCENTROIDA.—Test usually flattened, discoid, flexible; gills small; teeth not keeled; epiphyses not meeting; primary radioles without a cortex.

Order AULODONTA.—Test globe-shaped; gills well developed; teeth not keeled; epiphyses not meeting; primary radioles without a cortex.

Order STIRODONTA.—Test globe-shaped; gills well developed; teeth keeled; epiphyses not meeting; primary radioles without a cortex.

Order CAMARODONTA.—Test globe-shaped; gills usually well developed; teeth keeled; epiphyses meeting above the pyramid; primary radioles without a cortex.

Sub-class IRREGULARIA

Mouth variously placed on the lower surface, anus never central above, but lying in the posterior interambulacrum.

All four orders are represented in the New Zealand Cenozoic:

Order HOLECTYPOIDA.—Test globe-shaped or hemispherical, mouth central, ambulacra meridional and not modified into petals or phyllodes.

Order CASSIDULOIDA.—Test ovoid, mouth central, ambulacra more or less petaloid above and forming phyllodes below.

Order CLYPEASTROIDA.—Test discoid, mouth central, ambulacra forming distinct petals above but not phyllodes below.

Order SPATANGOIDA.—Test ovoid or heart-shaped, mouth anterior, ambulacra variable but usually forming petals.

Only the Cidaroida are discussed in this bulletin. The order includes three families. The Archaeocidaridae have four or more columns of plates in each interambulacrum, and are restricted to the Paleozoic. The Psychocidaridae have two columns of plates in each interambulacrum and non-perforate tubercles; the only known surviving species is restricted to the Bonin Islands. The Cidaridae, the only family represented in New Zealand Cenozoic faunas, have two columns of interambulacral plates and perforate tubercles.

Family **CIDARIDAE**

The following summarizes the chief structures likely to occur as fossils.

The Cidaridae, in common with other echinoids, have complex skeletons, the individual elements of which frequently exhibit generic and specific characters. In the living species *Goniocidaris umbraculum*, for example, there are at least three thousand separate skeletal plates and radioles, of some sixty different shapes and sizes, some with very elaborate microscopic detail. Of these, only some six hundred would normally be of paleontological significance—that is, several of them associated, or in some cases single elements or parts thereof, would be sufficient to give the generic and specific determination. Not all Cidaridae are so easy to recognize from isolated pieces; in such cases the sum of the characters exhibited by the parts has to be considered. Again, the systematic position of certain forms cannot be determined from the skeleton alone; these are best referred to *Cidaris* (*sensu lato*), not to be confused with *Cidaris* (*sensu stricto*). Such species are of value only as index fossils. Fortunately, most Australasian fossil Cidarids exhibit generic as well as specific characters.

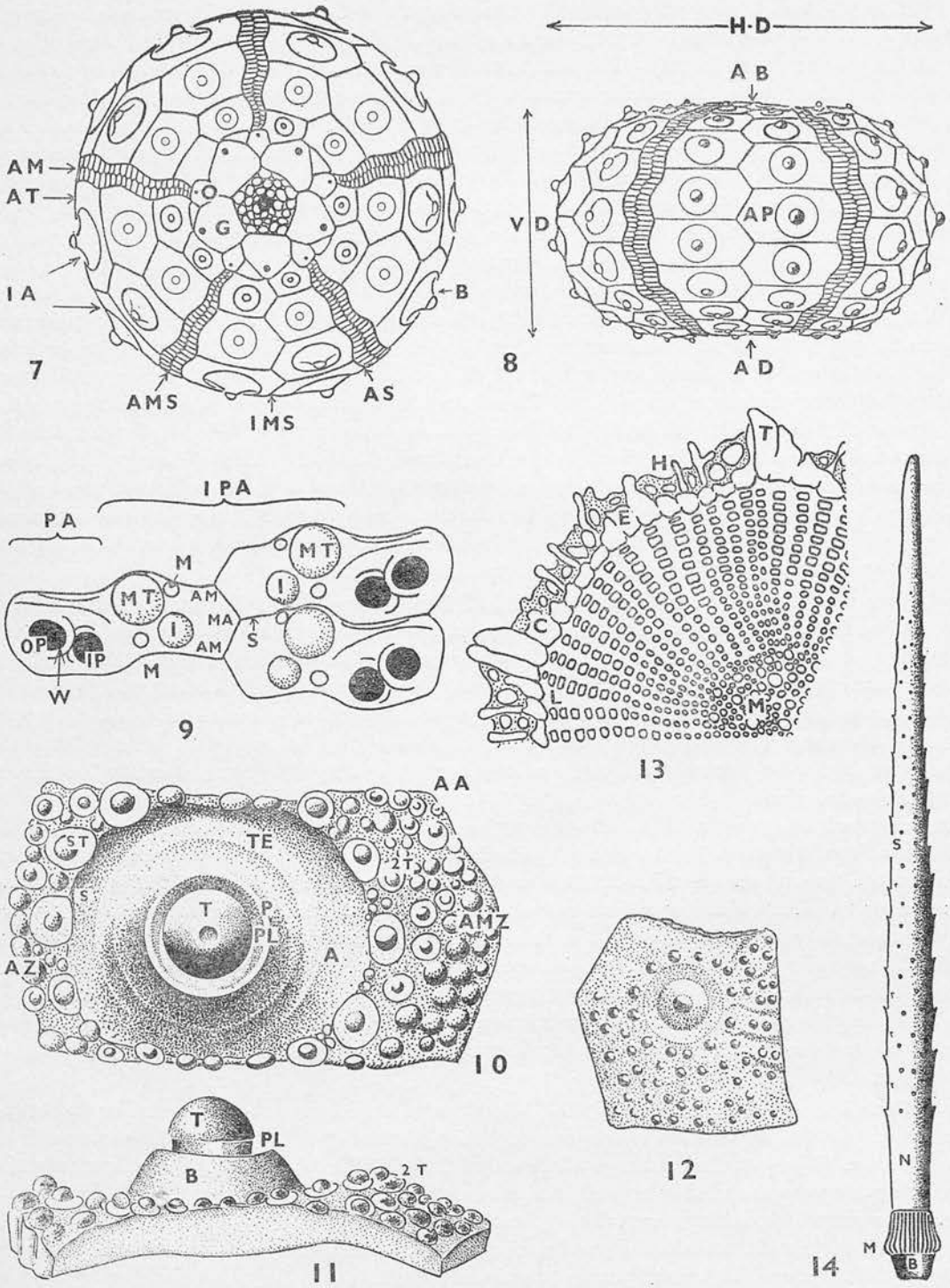
The only parts of the Cidarid skeleton which can usefully be employed in paleontology are whole or partial tests, ambulacral and interambulacral plates, and primary radioles. The description of fossils is accordingly confined to these elements, save in the exceptional case of *Notocidaris vellai*, where secondary radioles and pedicellariae occur as fossils.

The *test* (Text figs 7, 8) is the outer (but mesodermal) shell formed by twenty vertical columns of plates. Its upper surface, in the centre of which the anus and genital apertures are found, is termed *aboral*. The lower surface, surrounding the centrally placed mouth and *peristome*, is termed *adoral*. The dimensions of the test are expressed by the *horizontal diameter* (h.d.) and the *height* (ht.) (or vertical diameter, v.d.). The major circumference is always horizontal, and is termed the *ambitus*. Skeletal plates in the vicinity of the ambitus are described as *ambital* plates. Ten of the vertical columns of plates are arranged in five double, equally spaced meridional series called *ambulacra*. The ambulacra of Cidaridae are always relatively narrow, sometimes straight, more often sinuous. The remaining ten columns are disposed in five double, vertical series which alternate in position with the ambulacra. These are termed the *interambulacra* (I.A.). They form broad segments, and bear large prominent bosses.

The *ambulacra* (Text fig. 9) are divisible into an outer *pore zone* and an inner, broader *interporiferous zone*. The pore zone is distinguished by the presence of pores, two of which occur on each ambulacral plate, the *pore pair*. The two pores of a pore pair correspond to the points of ingress and egress of the circulating ambulacral fluid which enters each tube foot in the living animal. The two pores of a pair are usually more or less horizontally disposed, but in some forms they are obliquely inclined. They lie near the lower edge of the plate. If the pores of a pair are separated from each other by a distinct wall, they are described as *non-conjugate*. If they lie in a common groove, or if the wall between them is broken by a col, they are described as *conjugate*. The interporiferous zone is wider than the pore zone and is characterized by possessing various rounded *tubercles*. Adjoining the pore zone there occurs on each ambulacral plate a relatively large *marginal tubercle*. The vertical series they form is termed the *marginal series*. It may be straight or sinuous. On the inner side of the marginal tubercle may occur one or several tubercles, usually smaller, and often irregularly arranged; these are the *inner tubercles*. Both marginal and inner tubercles carry very small spines, called *ambulacral radioles*. A third type of tubercle may occur, very small, and irregularly scattered among the others. These are *miliaries*, and serve as points of attachment of *pedicellariae*. Pedicellariae are small grasping organs on various parts of the test; they have a complex structure, but their paleontological significance is slight. The borders of the ambulacral plate are the *sutures*. At the point where the neighbouring ambulacral plates of the two columns adjoin is the *median angle*, and above it and below it are the two *admedian angles*. The opposite, or outermost, border of the plate adjoins an interambulacral plate, and is called the *outer border*. The *horizontal sutures* separate neighbouring ambulacral plates of the same column.

Each *interambulacral plate* (Text figs 10, 11, 12) bears a single large prominence, the *boss*. Surmounting the boss is a *platform* on which is a rounded *tubercle* (or mamelon). The tubercle articulates with the primary radiole of the plate. It has a central *perforation*, from which in life a strand of ligamentous tissue runs to a corresponding perforation in the base of the acetabulum of the radiole. All Recent Cidaridae are *perforate* in this respect, unlike some other groups of echinoids. The platform is often surrounded by a low *parapet*, and its surface may be *crenulate* or *non-crenulate*. The boss sometimes arises from a *basal terrace*. It is surrounded by a broad, saucer-shaped shallow depresion, the *areole*, which is devoid of sculpture. The outer margin of the areole is somewhat sunken and is termed the *scrobicule*. It serves as the region of origin of the muscles which move the radiole. Surrounding the scrobicule, and situated at the level of the remainder of the plate, is a more or less continuous ring of smaller tubercles, the *scrobicular tubercles*. Each of these usually has a small areole, and in life carries a small *scrobicular radiole*. The remainder of the plate is usually covered by *secondary tubercles* and *miliaries*. The outer region, adjoining the ambulacrum, is termed the *adradial zone;* the inner region where the two interambulacral series of plates adjoin is the *admedian zone*. If there is a region of secondary tubercles between the areole and the upper suture, it is termed the *upper zone*. In other cases the areole may extend from the upper suture to the lower one, in which case the scrobicules are *confluent;* or the scrobicular rings of neighbouring plates may be *contiguous*.

The spines of Cidaridae (Text figs 13, 14) comprise large *primary radioles* carried by the largest tubercles, and smaller *secondary radioles* carried by the other tubercles. Only the former are of fossil importance. The *base* of a primary radiole articulates with the tubercle of its plate by means of a cup-shaped depression in its lower surface, the *acetabulum*. Radioles which articulate with crenulate tubercles are correspondingly crenulate around the margin of the acetabulum. Above the base is a more or less conspicuous *milled ring* and a *collar*, both of which are striated, and serve for the insertion of the muscle which arises from the scrobicule. Some radioles have a region just beyond the collar termed the *neck*. In all radioles the remainder of the spine is the long *shaft*. The shaft may be cylindrical or fluted or thorny; it usually tapers, but may expand into a blade or into a hollow trumpet-like structure, or the whole shaft may be converted into a cup-shaped organ. Such features are often of diagnostic importance. The microscopic structure of a primary radiole is complex. There is a central sponge-like mass of calcite for which no special name seems to have been given



TEXT FIGS 7 to 14. Structure of the Cidarid skeleton

Fig. 7. Test viewed from above: AM, ambulacrum; AMS, ambulacral median suture; AS, adradial suture of interambulacrum; AT, ambitus; B, boss; G, genital plate; IA, interambulacrum; IMS, interambulacral median suture; O, ocular plate.

Fig. 8. Test viewed from side: AB, aboral surface; AD, adoral surface; AP, ambital plate; HD, horizontal diameter; VD, vertical diameter (or height).

hitherto; it is termed here the *medulla*. Radiating from the medulla are many vertical lamellae or *septa*, united to one another by *trabeculae* which enclose *perforations*. The arrangement, shape, size, and number of these structures are of diagnostic value. Outside the *radial zone*, which comprises the foregoing structures, is a dense outer covering, the *cortex* (or ostracum). Opposite each radial septum a vertical groove or slit traverses the cortex, which thus appears to be divided into a number of vertical rods, here termed the *end-plates*. Ridges or thorns, etc., may be developed from thickenings of the cortex, or from both the radial zone and the cortex. *Cortical hairs* may form more or less anastomosing meshworks on the outer surface of the cortex or in the flutings of its outer surface.

The New Zealand Genera

The usual systematic keys to the genera of Cidaridae are not of much practical value in New Zealand paleontology, where the material is nearly always in a fragmentary state. The following notes may be found more useful. They are intended only for New Zealand material.

Dissociated Plates

A plate with a more or less naked and depressed suture, especially at the median and admedian angles, indicates either *Ogmocidaris* or *Goniocidaris*. The specific determination must now be made from keys given under those genera. If radioles are available they will also determine the genus, since those of *Ogmocidaris* are tapering, slender, and cylindrical, whereas those of *Goniocidaris* will include branched forms with lateral wings or spurs and cup-shaped forms. *Ogmocidaris* is as yet unknown in the fossil state.

Strongly crenulate interambulacra with confluent areoles indicate *Histocidaris*.

Large interambulacral plates with scrobicular tubercles bearing inner and outer elevations indicate *Phyllacanthus*. The ambulacral plates of this genus have close-set conjugate pores, lying in a groove.

Stereocidaris plates are tumid with a broad upper zone, but difficult to place with certainty unless the aboral plates are also present. The latter are characterized by having only rudimentary areoles and bosses. Radioles may aid the determination, if present.

Plates of *Prionocidaris* and *Eucidaris* have not been recognized from the New Zealand Tertiary as yet. In the former genus the pores are conjugate and set wide apart in a deep groove. In the latter the determination can only be made from associated radioles.

Radioles

More or less club-shaped radioles with shafts ending in a crown-like structure surmounted by a central prominence indicate *Eucidaris*.

Radioles with a cylindrical shaft and a strongly crenulate base belong to *Histocidaris*.

Fig. 9. Ambulacrum: AM, admedian angle; I, internal tubercle; IPA, interporiferous area; IP, internal pore; M, miliary; MA, median angle; MT, marginal tubercle; OP, outer pore; PA, poriferous area; W, wall.

Fig. 10. Interambulacral plate: A, areole; AA, admedian angle; AMZ, admedian zone; AZ, adradial zone; P, parapet; PL, platform; S, scrobicule; ST, scrobicular tubercle; T, primary tubercle; TE, basal terrace; 2T, secondary tubercles.

Fig. 11. Same interambulacral plate, in side view.

Fig. 12. Upper interambulacral plate with rudimentary areole.

Fig. 13. Transverse section of shaft of radiole: C, cortex; E, end-plate of cortex; H, cortical hair; L, lamella (or septum) of radial zone; M, medulla; T, cortical thorn. ×75.

Fig. 14. Primary radiole: B, base; C, collar; N, neck; M, milled ring; S, shaft. ×5.

Fig. 7 and 8 are generalized diagrams. Figs. 9, 13, and 14 are *Ogmocidaris benhami* Mrtsn. Figs. 10 and 11 represent an ambital plate of a specimen (EC 152) in the collection of the N.Z. Geological Survey, from GS 5516, of uncertain systematic position; 8·5 mm. x 5 mm. Fig. 12 is from the holotype of *Stereocidaris striata* (Hutton), probably the second interambulacral plate from the apical region, the uppermost plate apparently missing from the specimen. Although these specimens are here utilized to illustrate Cidarid anatomy, fuller reference to them is made under the systematic sections on *Ogmocidaris*, *Stereocidaris*, and *Eucidaris*.

If the shaft is cylindrical and tapering, bearing minute thorns derived from the cortex only, and with the collar not distinctly separated from the milled ring, the radiole belongs to *Ogmocidaris*. The whole radiole does not exceed *ca* 35 mm. in length in this genus.

A massive cylindrical pencil-like spine, up to 10 mm. diameter and up to 200 mm. in length, indicates *Phyllacanthus*. Even a small fragment can be identified by the transverse section, which is characteristic (see Plate 10, A, D).

A shaft with more or less paired lateral outgrowths, spurs, wings, and flattened processes points to *Goniocidaris*. If cup-shaped radioles or plates with naked admedian areas are present, the diagnosis is confirmed.

A shaft with thorny outgrowths, and with a thin cortex, characterizes the species here provisionally referred to *Prionocidaris*.

Longitudinal flutings, longitudinal rows of delicate thorns arranged in alternating series, a well-developed cortex, and no flattened outgrowths or associated cups suggest *Stereocidaris*. The specific determination should not be difficult, but there is some uncertainty as to the generic placing of the group, which is here treated as *Stereocidaris*.

Radioles are especially valuable for the amount of minute detail they provide. Even though their generic position is sometimes uncertain, their specific peculiarities render them suitable for use as index forms in stratigraphy.

Genus **Histocidaris** Mortensen

Mortensen, Th. 1903. "*Ingolf*" *Echinoidea*, l, p. 30.
Type species *Porocidaris elegans* A. Agassiz 1879.

Tubercles perforate, strongly crenulate. Pores non-conjugate. Primary radioles cylindrical, collar short. Oral primaries strongly serrate, curved. Areoles shallow.

Histocidaris mckayi sp. nov. (Plates 7, A–J; 9, D; 12, G; 13, C; 14, E)

Cidaris, A. McKay, *Rep. Geol. Explor. 1882*, p. 70.
Cidaris, Waihoa [*sic*], South Canterbury; J. Hector, *Cat. Geol. Exhib. N.Z. Court, Col. Exhib.*, 1886, p. 57, Fig. 2.
Rhabdocidaris, R. Tate, *Rep. Geol. Explor. 1892–3*, 1894, p. 121.
Cidaris sp. nov., Waihao Limestone, J. Park, *Geology of N.Z.*, 1910, p. 140, Fig. 72.

Holotype (Plate 13, C)

A test with attached radioles, in the Geology Department, University of Otago, coll. C. R. Laws, Waihao Limestone, near Waihao Forks—Duntroonian (lower Oligocene).

TEST: Subspherical, flattened above and below, circumference rounded; h.d. 47 mm., ht. *ca* 30·0 mm.

AMBULACRA: *Ca* 25 per cent of I.A., distinctly sinuate above, nearly straight at the ambitus. Near the ambitus the interporiferous zone is *ca* twice as broad as a pore zone, but near the apical system it is much narrower than a pore zone. Marginal series of tubercles very regular, the tubercles contiguous or nearly so, occupying about half of the interporiferous zone over most of the ambulacrum, but occupying most of the interporiferous area near the apical system. Inner tubercles present, but indistinct on holotype (see, however, Paratype, below). Pores sub-equal, the outer pore slightly larger than the inner. A narrow elevated wall coils about the inner margin of the outer pore, separating it from the inner pore, partly overhanging the latter, which also lies at a somewhat lower level.

INTERAMBULACRA: I.A. plates *ca* 10, the lowermost hidden on the holotype by attached oral primary radioles. Areoles transversely elliptical on the ambital and subambital plates, subcircular above. All areoles save the uppermost one or two are confluent. Primary tubercles strongly

crenulate, 13 or 14 crenulations. Median area very narrow, always less than one-quarter of the width of an areole, on the uppermost plates all but obliterated by the large areoles which here occupy nearly all the plate. Edge of the areole slightly elevated. Scrobicular tubercles distinct, occupying the inner and outer boundaries of the areoles, but mostly lacking from the transverse upper and lower margins where the successive areoles are confluent. Secondary tubercles similar to the scrobicular tubercles, occupying all the median and outer areas, leaving no bare median or adradial spaces.

APICAL SYSTEM: 15·0 mm. diameter, *ca* one-third h.d. Apical plates lost.

PERISTOME: Obscured (but see Paratype, below).

PRIMARY RADIOLES: Cylindrical, the shaft *ca* 2·0 mm. diameter, milled wheel prominent, 4·0 mm. diameter. Oral primaries *ca* 15·0 mm. long, flattened, with serrated edges (Plate 7, I, J).

Paratypes: N.Z. Geological Survey Collection.

GS 74: Calcareous greensands, Weka Pass, Canterbury, coll. J. Hector, 1867; Julius von Haast, 1869; Alexander McKay, 1874. Isolated plates and radioles. EC 141. Duntroonian.

GS 243: Fan Coral Bed, Trelissick Basin, coll. J. D. Enys, 1866, 1879. Isolated radioles. EC 144. Duntroonian.

GS 482: Waihao Limestone (glauconitic), Waihao River, coll. A. McKay, 1880. Portions of tests. EC 137, 143. Other material from this locality was collected by A. C. Amies recently. Duntroonian.

GS 484: Maerewhenua Limestone, Pigeon Rock, Waitaki Valley, Otago, coll. A. McKay, 1880. Portions of tests, isolated plates and radioles. EC 127, 140, 142. Waitakian.

KAKANUI: Three interambulacral plates with associated ambulacral plates, in very fine condition (Geology Department, University of Otago). Waitakian.

CAPE FAREWELL: An extremely eroded test fragment, in the Otago University, apparently to be referred to this species (crenulation lost). Duntroonian–Waitakian.

Stratigraphical Range

Duntroonian to Waitakian, lower to middle Oligocene.

Further Account

Ambulacral plates from Kakanui (Plate 7, B) illustrate their structure more distinctly than does the holotype. There is a small outer tubercle above the outer pore, and also one inner tubercle within the marginal tubercle, somewhat smaller than the latter.

In larger tests, for example, the paratype from Waihao in the N.Z. Geological Survey Collection, illustrated in Plate 14, E, there are approximately 12 interambulacral plates to a column, and 80 or more ambulacrals. In a fragment which exhibits the whole series in both columns, the following were the numbers of ambulacrals observed in sequence opposite each of the 12 interambulacrals, passing from the adapical extremity downwards to the peristome: 6, 8, 10, 12, 10 (ambitus), 9, 8, 6, 5, 4, 3, 2. The peristome is seen in oral aspect in one very eroded paratype (EC 143). It is evident that the peristome cannot exceed one-quarter h.d., and thus is smaller than the apical system.

Some radioles show a weak fluting, six or seven very shallow longitudinal grooves separating equally shallow, broad, rounded ridges. Following are measurements from a typical radiole; base to milled ring, 2·0 mm.; milled ring to top of neck, 4·0 mm.; diameter of base, 2·25 mm.; diameter milled ring, 3·5 mm.; shaft at top of neck, diameter 2·0 mm.; internal diameter of acetabulum, 1·5 mm.; external diameter of acetabulum, 2·25 mm. Some shafts, fragments only,

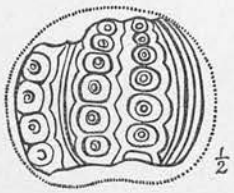
lacking the basal structures, reach diameters of 3 and 4 mm. The milled ring may reach 5 mm. diameter. It is always very prominent, and imparts a characteristic appearance to the radiole. The milled ring is very finely striate, the collar smooth.

The transverse section of the radiole is typically that of *Histocidaris*, and thus is easily distinguishable from that of all other Cenozoic cidarids so far known from New Zealand. The medulla (Plate 9, D) is extensive, coarsely perforate, reaching about midway out to the periphery. The radial zone is compact, the perforations circular, smaller without than within, about 16 to the series in a typical spine, well separated, the septa and trabeculae thick. Cortex showing shallow ridges and depression, or almost smooth. Cortical channels distinct, inner border of cortex irregular, outer surface even, without hairs.

Since *Histocidaris* has hitherto been unknown from the New Zealand area, either Recent or fossil, it is desirable to stress that the characters of this species point very strongly to that genus, and to no other. One feature, probably a generic character of *Histocidaris*, is the manner in which the elevated wall between the pores coils around the outer pore. It can be seen in the photographic figures in Mortensen's 1928 monograph, but his drawings on Plate LXVIII do not show the feature clearly. All the characters of *mckayi* point to *Histocidaris* rather than to any other of the three Recent and several fossil genera which have crenulate tubercles. *Acanthocidaris* has subconjugate pores, and both *Acanthocidaris* and *Porocidaris* have radioles with a long collar. *Dicyclocidaris*, *Porocidaris*, *Polycidaris*, and *Procidaris* are all eliminated on the ground of major differences in test structure. *Plegiocidaris*, *Paracidaris*, and *Rhabdocidaris* are distinguished by obvious radiole characters, and in any case, like *Dicyclocidaris*, are probably restricted to the Mesozoic.

The majority of the living species of *Histocidaris* are restricted to the Pacific. The genus is well represented in the seas to the north and east of Australia, but it has not yet been found in New Zealand, nor is it known as a fossil in Australasia. The present record is consistent with Mortensen's conclusion (based on the distribution of living species) that the Malayan–Australian area was the original home of *Histocidaris*. Lambert (1932) records a species of *Histocidaris* from the Miocene of Egypt, and (1931) another from the upper Tertiary of Algiers.

Hector's 1886 copper plate of " *Cidaris* from Waihoa ", listed above, measures *ca* 3 cm. across, and is too crude for identification. When compared with the photograph of the specimen EC 137 from Waihao illustrated in Plate 14, E, of the present bulletin, a general similarity in outline is



TEXT FIG. 15. " Cidaris (Waihoa, South Canterbury)." After Hector (1886, Fig. 19a, 2, p. 57). Probably *Histocidaris mckayi* Fell; compare with specimen EC 137 (Plate 14, E), collected by Alexander McKay at Waihao in 1880, and now in the collection of the New Zealand Geological Survey

observable. The specimen, now in the N.Z. Geological Survey, was collected by Alexander McKay in 1880. It seems likely that this was the specimen used by Hector for his illustration six years later. The figure here reproduced is the only representation of a New Zealand fossil Cidarid hitherto published during ninety years of systematic geological exploration. It was republished in 1910 in Park's *Geology of New Zealand*.

Genus **Stereocidaris** Pomel

Pomel, A. 1883. *Classification méthodique et genera des Echinides vivants et fossiles, p. 110.*
Type species *Cidaris cretosa* (Mantell) Cotteau.

Test solid, usually very closely tuberculate. Rarely more than seven interambulacral plates in a series; from one to three of the upper interambulacral plates with the areole, the primary tubercle, and the radiole usually rudimentary. The areoles deep, generally well separated, even those on the oral side. Interambulacral plates very high, especially the upper ones, with a broad

space covered with small miliaries between each two successive areoles. Usually one or several more or less distinct grooves or impressions in the upper horizontal sutures of the interambulacra, and usually a small but fairly distinct groove at the admedian end of the ambital horizontal sutures of the interambulacra. Ambulacra in general conspicuously sinuate. Pores non-conjugate, the wall usually forming a low, rounded crest. Madreporite not distinctly enlarged. Primary radioles often flaring at tip, the shaft usually with a spongy coat of hairs, collar short, neck very conspicuous, about twice as long as the collar.

Cidarid remains referable to *Stereocidaris* occur in the New Zealand Oligocene and as fragments in the middle Pliocene (Nukumaruan). It is not certain whether we have to deal with one long-ranging lineage, or whether the Pliocene form represents a second stock. The Pliocene form seems to have reached a larger size than the earlier one, and, meantime at least, it seems advisable to treat the two forms as distinct species.

KEY TO THE NEW ZEALAND SPECIES

About 12 ambulacral plates opposite the largest interamb plate .. .. *striata.*
About 19 ambulacral plates opposite the larger interamb plates .. .. *hutchinsoni.*

NOTE.—Radioles of *S. striata* are not known with certainty, but radioles attributable to *S. hutchinsoni* are common in the Nukumaruan Stage and can easily be recognized from the illustrations on Plates 6 and 9.

Stereocidaris striata (Hutton). (Plates 1, A; 6, E, I, M; 9, A; 11, A; 14, D, F)

Cidaris striata Hutton, F. W., *Cat. Tert. Mollusca & Echinodermata of N.Z.*, p. 38, 1873.
Leiocidaris australiae Hutton, F. W., *Trans. N.Z. Inst. 19:* 406, 1887.
Cidaris (Leiocidaris) australiae Tate, R., *Rep. Geol. Explor. N.Z., 22*, p. 126, 1894.
" *Cidaris* " *striata* Hawkins, H. L., *Vid. Medd. dansk Natur. For. 79:* 409, 1925.
NON *Leiocidaris australiae* Duncan, P. M., *Quart. J. Geol. Soc. Lond.*, 1887 (equals *Stereocidaris australiae* (Duncan) Chapman and Cudmore, 1934).
NON *? Cidaris striata* Hutton, Tate 1894 (equals *Stereocidaris australiae* (Duncan) Chapman and Cudmore, 1934).

Holotype (Plate 14, D, F)

A somewhat crushed, broken, and eroded test, EC 136 in the collection of the N.Z. Geological Survey, from Brighton, south-west Nelson—Duntroonian (lower Oligocene).

TEST: Subspherical, apparently somewhat flattened above, h.d. *ca* 50·0 mm., ht. *ca* 28·0 mm. (certainly not less, possibly more—the test has suffered some compression).

AMBULACRA: Somewhat sinuate, though not markedly so, *ca* 20 per cent of the width of the interambulacra. Interporiferous area (Plate 1, A) about twice the width of a pore zone. Marginal series of tubercles regular, prominent, but not contiguous. Internal tubercles smaller than marginals, crowded, somewhat irregularly disposed. Interporiferous area flat, somewhat raised above the level of the pore zones.

INTERAMBULACRA: Six or seven plates to the column, upper plates higher than broad, ambital plates as high as broad, subambital plates somewhat broader than high. Areoles deep, well separated, save for the two lowermost, which are confluent. Outer borders of areoles steep, wall-like, hence casting very well defined shadows in side illumination (cf. Plate 14, F). Scrobicular tubercles on the larger plates somewhat uneven in size and arrangement, but scrobicular rings nevertheless prominent, overhanging the areole to a varying degree. On smaller plates, scrobicular tubercles less prominent. Areoles all circular, save for the smallest proximal one, which is transversely oval. On the upper and ambital plates, areoles lie nearer to the lower suture than to the upper. Uppermost areole and tubercle rudimentary (Plate 11, A). Secondary tubercles very numerous, much smaller than the scrobicular tubercles, densely crowded over the median, upper, and outer areas. Transverse sutures conspicuous above, sunken. On ambital plates, transverse sutures conspicuously sunken admedially, and also to some extent at their outer (adambulacral) extremities.

By combining data from the several columns the following composite tabulation may be derived:

Interamb. Plate	Width (mm.)	Height (mm.)	Diameter of Areole (mm.)	Number of Amb. Plates Opposite
No. 1 (adapical)	Missing or broken on all columns			?5
No. 2	7·0	8·0	3·0	11
No. 3	12·0	9·5	7·5	12
No. 4	11·0	8·0	6·5	11
No. 5	7·5	5·5	4·5	9
No. 6	4·5	3·0	2·5	7
No. 7 (adoral)	3·5	2·0	2·5 × 2·0	4

APICAL SYSTEM and PERISTOME: Unknown.

In the Canterbury Museum there is a fragmentary test from Broken River which may be referred to this species. It comprises the ambital and subambital portion of an interamb, with attached ambulacrals. It is from a somewhat larger individual than the holotype; the h.d. may have been nearer 60 mm. It otherwise resembles the holotype, and, like it, is of Duntroonian age.

RADIOLES: No radioles are associated directly with either of the tests. Probably some radioles from lower and middle Oligocene horizons should be referred to the species. A graduated sequence of forms compares closely with some of the radioles which Chapman and Cudmore (1934) have referred to *Stereocidaris australiae* (Duncan). They range from cylindrical, tapering forms up to 3 mm. in diameter and more than 26 mm. long, to somewhat flattened forms. All types have fluted, longitudinally granulated, or slightly thorny sculpture. In the more flattened forms the sculpture is more pronounced on the two opposed edges of the shaft. On well-preserved bases a delicate crenulation may be observed on the edge of the acetabulum. Chapman and Cudmore (1934) note the same condition in *Stereocidaris australiae*.

The following radioles are provisionally referred to this species:

GS 311: Curiosity Shop, Rakaia River, Canterbury, some thirty primary radioles, EC 145, coll. A. McKay, 1879. Also from this locality, three radioles in the Canterbury Museum, probably collected by von Haast—Duntroonian–Waitakian.

GS 2225: Burnside marl-pit greensand, part of a radiole, EC 163 (Plate 6, M), coll. M. Ongley—Waitakian.

GS 5516: Allday Bay, base of Campbell's Beach limestone, three fragments of radioles, EC 123–124 (Plates 6, E, I; 9, A), coll. J. Marwick—Whaingaroan.

GS 5636: Earthquakes, Duntroon, radioles EC 166, coll. M. Gage—Duntroonian.

A fragment of a radiole from Pitt Island, Chatham Group, now in the Canterbury Museum, is possibly of this species.

Stratigraphical Range

Whaingaroan to Waitakian, Oligocene.

Remarks

Stereocidaris striata, the only New Zealand Tertiary Cidarid hitherto described, has had a checkered history since Hutton described it in 1873. His diagnosis consisted of only five lines, and included the quite misleading statement that there are no ambulacral tubercles. As the holotype has been preserved, it is possible to retain Hutton's name.

Hutton later lost faith in his species, and in 1887 declared it to be a synonym of *Leiocidaris australiae* Duncan (though *striata* had priority). Tate (1894) concurred with Hutton's change. Hawkins examined the holotype in 1925, and commented in a " Note " published by Mortensen (1925): " Hutton's ' *Cidaris* ' *striata* has nothing to do with Duncan's *Leiocidaris australiae*, but seems to be more akin to *Goniocidaris* or to some Cretaceous group such as *Typocidaris* ". The latter was probably his final preference, for the type was returned to New Zealand twenty-five years later with the identification *Goniocidaris* struck out, and *Typocidaris* substituted.

In 1928 Mortensen declared *Typocidaris* a synonym of *Stereocidaris*, so that Hawkins' determination was substantially in agreement with the opinion expressed here.

In 1934 Chapman and Cudmore revised the Australian Tertiary Cidaridae, and showed that Duncan's *Leiocidaris australiae* must be referred to *Stereocidaris*, but did not comment on the New Zealand species.

Hawkins' opinion that the two Australasian species were not closely related was no doubt influenced by Duncan's statement that the ambulacral pores in *Leiocidaris australiae* are conjugate. This would be the case if *australiae* were really referable to *Leiocidaris* (a synonym of *Phyllacanthus*). However, Chapman and Cudmore showed conclusively that Duncan's statement was a mistake, and that the pores are non-conjugate. Although the Australian material is variable, especially in regard to the number of rudimentary areoles on the upper plates, a conspicuous difference from the New Zealand form lies in the fact that the scrobicular rings on the lower surface are elliptical and merge together; in *S. striata* the areoles are well separated, and only the lowest two are contiguous. There can be little doubt, however, that the two forms are congeneric.

More obscure are the relationships of a Cidarid occurring in the Nukumaruan (middle Pliocene) beds of New Zealand, and at present known only from isolated spines and two coronal plates, one of them with attached ambulacral plates. *Stereocidaris* seems to be its most likely generic position.

Stereocidaris hutchinsoni sp. nov. (Plates 6, A–D, F–H, J–L; 9, E)

Holotype (Plate 6, G and H)

An ambital interambulacral plate with attached ambulacral plates, EC 119 in the N.Z. Geological Survey Collection; from GS 4259, fine sandstone below Kuranui limestone, east of Waitotara River, 1 m. 35 ch. at 104° from Trig P, coll. J. Marwick and C. A. Fleming—lower Nukumaruan (Pliocene).

Interambulacral Plate: Width 14·0 mm., height 11·5 mm. (a test of at least 50·0 mm. diameter is implied). Areole circular, 8·0 mm. diameter, lying nearer the lower suture than the upper, but not confluent, and indicating well-separated scrobicular rings. Areole deep, with steep outer wall, somewhat overhung by the scrobicular tubercles. Scrobicular tubercles prominent, on elliptical bases. Primary tubercle prominent, hemispherical, perforate, non-crenulate. Median, upper, and adradial areas densely covered by small crowded miliaries, which tend to form linear series along the adradial margin. The plate is tumid, its upper and admedian borders especially sunken below the tumid central region, indicating, therefore, depressed suture-lines. No naked area along the sutures.

Ambulacral Plates (Plate 6, B): Nineteen ambulacral plates opposite the interambulacral plate. Ambulacrum distinctly sinuate. Interporiferous area raised, about as wide as the pore-zone on the single series of amb plates preserved, thus indicating a complete ambulacrum twice as wide as the pore-zone. Marginal tubercles prominent, regularly arranged in contiguous series, but not crowded. Inner tubercles two or three to each plate, the outer one often nearly as large as the marginal, the inner one or two smaller, crowded. Pores non-conjugate, almost circular, separated by a distinct elevation.

Further Account

From the type locality a single spine is known. This is the shaft and part of the collar of a primary radiole, length 25·0 mm., diameter at collar 2·0 mm., diameter near apex 3·5 mm. The radiole is somewhat flattened, flaring towards the extremity, as the dimensions indicate. Its sculpture comprises longitudinal ridges and flutings, two or three to the millimetre, the ridges replaced by linear series of granules near the base.

Similar spines, and others of the same type but of various forms, including an oral spine, are found in other Nukumaruan localities. They are usually found in creek beds and so are more or less eroded. The shape varies from cylindrical and tapering to flattened, almost spatulate (Plate 6, A, C, D, J, K, L).

The cross-section (Plate 9, E) shows a central core of medulla which extends to *ca* one-third of the way out to the periphery. Radial zone of varying thickness along different radii, extending into the surface ridges, the laminae widest within, the perforations smallest within, increasing in size towards the exterior. Extra interpolated laminae appear at various distances out, especially along the radii corresponding to the surface ridges. Cortex very deeply fluted and ridged, thickest on the ridges. Cortical hairs form a spongy mass which fills most of the surface flutings, covering all the cortex save that on the ridges.

Relationships

The depressed sutures of the holotype point to *Goniocidaris* or *Stereocidaris*. The absence of naked areas, the circular, well-separated areoles, the extensive upper area on the interambulacral plate, and the general appearance of the plates suggest *Stereocidaris*, and certainly eliminate *Goniocidaris*. The non-conjugate pores, and the fact that the pores are not oblique, eliminate other possible genera, including the whole Antarctic group (which might conceivably have entered New Zealand waters in the cool Nukumaruan phase). The cross-section of the spines also suggests either *Goniocidaris* or *Stereocidaris*, but the absence of other Goniocidarid characters (such as basal or apical disks or cups on the radioles, and spurs), together with the rather large size, seem to eliminate *Goniocidaris*. Accordingly the fragments are referred to *Stereocidaris;* but the generic position cannot be precisely settled until more information is available—for example, whether the upper areoles are rudimentary. For these reasons it would be fruitless to attempt to assess the relationship between this species and the foregoing beyond noting the general similarity in structure.

Paratypes

Omatua Creek-bed, Rissington, Hawke's Bay: Primary radioles, coll. F. Hutchinson, H. B. Fell, 1932–1947. Nukumaruan.

GS 5752: Olrig Stream-bed, Maraekakaho, Hawke's Bay. Primary radioles, EC 118, 121, 122, 125, 126, coll. H. B. Fell, 1947. Nukumaruan.

GS 5435: Below Whakapiru Road, Maraekakaho Survey District, coll. T. L. Grant-Taylor, radioles, EC 150. Nukumaruan.

GS 5436: In Creek near Okauawa Stream, Matapiro Survey District, radiole, EC 151, coll. T. L. Grant-Taylor. Nukumaruan.

Western Side of Ruahine Range: One mile up Saddle Road from Ashhurst to Woodville, radioles, coll. J. W. Brodie, 1951. These spines were found in a muddy sandstone containing fossil Mollusca, indicating a depth of *ca* 25 fathoms (C. A. Fleming)—upper Nukumaruan.

GS 5754: Sheet N 162/013306, tributary of Martin's Stream, Huangarua Survey District, radioles, coll. J. D. Cowie, 1948—lower Nukumaruan.

Stratigraphical Range

Apparently restricted to the Nukumaruan, middle Pliocene, but it is possible that this species still survives.

Genus **Goniocidaris** Agassiz & Desor

Agassiz, L., and Desor. 1847. *Annales des Sciences, 3, ser. 6–8.*
Type species *Cidarites tubaria* Lamarck.

Test usually flattened. Ambulacra usually with a rather broad interporiferous zone; pores close together, not conjugate, separated by a more or less distinctly elevated wall. Median part of the horizontal sutures sunken, forming a more or less conspicuous groove both in the ambulacra and the interambulacra, the grooves often connected by a deepened, naked furrow along the vertical mid-line. Primary tubercles perforate, non-crenulate in Recent species, sometimes partly crenulate in older Tertiary forms. Primary radioles often expanded basally into a disc, shafts sometimes with paired spurs at the base. Apical radioles usually modified into cup-shaped or umbrella-shaped structures. Surface of radioles bearing an outer coat of fine, more or less anastomosing hairs, with free terminations. Collar very short.

The above diagnosis is mainly based on Mortensen (1928), but is slightly modified through later studies of Chapman and Cudmore (1934) and of the writer. The oldest representatives of the genus occur in the Australian and New Zealand lower Tertiary. Recent species range the Indo–West-Pacific, with Malaya as the focal point. One Recent species was already known from New Zealand, and to this two Tertiary forms may now be added.

Key to the New Zealand Species

1. Test small, depressed, horizontal diameter less than 20 mm. Secondary tubercles of the interambs represented only by the scrobicular ring. Oligocene .. *pusilla.*
   Test of medium size, horizontal diameter more than 20 mm. .. .. 2.
2. Areoles circular, well separated from one another by broad horizontal zones of miliary tubercles. Spines include robust radioles with flattened, lateral excrescences. Oligocene .. .. *hebe.*
   Areoles transversely elliptical, almost confluent, separated from each other only by a very narrow, horizontal series of rudimentary scrobicular tubercles. Recent .. .. *umbraculum.*

Goniocidaris hebe sp. nov.* (Plates 4, A–J; 7, D; 8, D)

The material includes coronal plates and radioles; as the latter are the commoner fossils, and usually show pronounced and easily recognizable specific characters, one radiole has been selected as the holotype. The generic position, however, is determined by the assemblage of characters exhibited by the fossils, namely, the cup-shaped apical spine, terminal cups on some radioles, and transverse and vertical sutural grooves on the coronal plates.

Holotype (Plate 4, C)

A primary radiole, EC 110, in the N.Z. Geological Survey Collection; from GS 311, Curiosity Shop, Rakaia, coll. A. McKay, 1879. Length 17·0 mm., the distal extremity broken off. Diameter at base 1·25 mm. Diameter of milled ring, 3·0 mm. Diameter at top of collar 2·3 mm. Height of collar 1·0 mm. The shaft widening distad, the distal half expanded on either side into two broad, flattened, fan-like sheets, *ca* 10·0 mm. across. Below the fan-like expansions on one side of the shaft, are several thorns. The fan-like processes are not quite diametrically opposite to each other, but instead shape a concave surface on the side on which the thorns occur, and a convex surface on the other side. The distal end of the shaft is flattened, 4·0 mm. across and 2·0 mm. deep.

Further Account

Plate 4, A–I, illustrates selected paratype radioles from the type locality. Figure A is an apical cup, finely striated on the outer surface, the striae bearing minute thorns. The cup is *ca* 9·0 mm. diameter, *ca* 3·0 mm. deep. Less developed terminal cups are present also on other

* Hebe—cup-bearer.

radioles (Figs E, G) with fluted shafts bearing paired excrescences, the flutings shaping a coalesced circlet of thorns at the distal end. Various degrees of flattened lateral outgrowth are seen in figures B and H. One fragment, EC 132, apparently also referable to this series, is peculiar in having a greatly expanded milled ring (reminiscent of the genus *Homalocidaris*); this structure is clearly atypical, perhaps pathological. It comes from the type locality, and, like some of the coronal plates, shows partial crenulation on one side of the acetabulum; thus it is virtually established that it belongs to this species, since none other of appropriate structure occurs in the lower Oligocene, so far as is known (see Fig. 8d).

Coronal plates of *Goniocidaris*, all referable to one species, occur in the type formation and locality. They are of appropriate size for the radioles described above; some radioles, as mentioned, show traces of crenulation on one side of the acetabulum, and some coronal plates show similar partial crenulation on one side of the platform. Furthermore, the apical cup, and terminal cups on some radioles, indicate the same genus as do the coronal plates, *Goniocidaris*. Consequently all these structures are referred without hesitation to one species.

The coronal plates (Plate 4, F, J) have a circular areole, well separated from the margins, a broad zone of miliaries extending across the upper part of the plate. Scrobicular tubercles are fairly well defined, somewhat irregular, larger than the miliaries; the scrobicular ring is complete, and the upper and lower scrobicular tubercles are not rudimentary, but as well developed as the others. The upper suture is naked and depressed across the whole width of the plate, as in *Stereocidaris*. In the larger plates (Fig. J) there is also a vertical depressed, naked medial margin, which is continuous with the upper horizontal depression, so that the general character is that of *Goniocidaris*. Measurements: Larger plate, width 8·5 mm., height 7·0 mm., diameter of areole 4·75 mm. Smaller plate, width 6·5 mm., height 5·5 mm., diameter of areole 3·5 mm.

Relationships

The resemblance between this species and the Australian lower and middle Tertiary form *Goniocidaris prunispinosa* Chapman and Cudmore is rather evident. The spines illustrated by these authors in their Plate XIII (1934) very much resemble those of the present species. Nevertheless, quite pronounced differences exist, including the following:

(1) The coronal plates of *hebe* have a greater height/width ratio.

(2) The deeply sunken upper suture of *hebe* (a *Stereocidaris*-like feature) is not matched in *prunispinosa*.

(3) The scrobicular ring is elliptical in *prunispinosa*.

(4) The spines of *hebe* have a relatively greater lateral expansion, and the apical cup in *hebe* is shallower than in *prunispinosa*.

Among the more notable resemblances between the two species is the fact that some plates are occasionally found crenulated, the crenulation occurring on only about half or two-thirds of the platform, the remainder being smooth; also, the presence of flattened lateral extensions on the radioles is a peculiarity of both species.

Localities

GS 311, Curiosity Shop, Rakaia River, Canterbury, coll. A. McKay, 1879. Holotype and figured paratypes, plates, and radioles, all in the collection of the N.Z. Geological Survey, EC 108–117. Duntroonian–Waitakian.

GS 172, Hutchinson's Quarry, Oamaru, coll. A. McKay, 1876; a collection of fragmentary radioles, EC 139, from this locality, now in the N.Z. Geological Survey Collection, is apparently to be referred to this species. The radioles include only the more slender types, but as a number of them show lateral expansions of much the same type as in *hebe* s.s. they may all be referred to the one species meantime. It is possible that fuller collecting will reveal that the Hutchinsonian form

is distinct; but, bearing in mind the great variety in radiole-forms exhibited by single species of *Goniocidaris*, it is not possible to distinguish separate species, or even varieties, in the material now available.

Stratigraphic Range

Lower and upper Oligocene, Duntroonian to Hutchinsonian, but not yet known from the intervening Otaian.

Goniocidaris pusilla sp. nov. (Plates 5, H; 13, D; 14, C)

Holotype

A test with associated spine in the Geology Department, University of Otago.

TEST: Small, very depressed, horizontal diameter 10·0 mm., height 5·0 mm.

AMBULACRA (Plate 5, H): *Ca* 25 per cent of I.A., straight. Near the ambitus the interporiferous zone is *ca* four times as broad as a pore zone. The marginal series of tubercles is very regular. Each marginal tubercle lies against the upper border of the amb plate, the latter having its upper suture markedly bulging upwards to accommodate the tubercle. The tubercles are widely separated from each other by bare intervening spaces, about equal in width to the diameters of the tubercles themselves. A smaller internal tubercle lies beside, and somewhat below, the marginal tubercle. The inner one-third of each amb plate is bare and sunken. The pores are circular, the outer member of each pair separated by a curved, raised wall from its inner neighbour; the pore pairs lie near the lower border of the plate.

INTERAMBULACRA (Plate 5, H): I.A. plates either six or seven to a series, the areoles confluent on the lowermost plates, with the bases of their bosses almost contiguous. Areoles more or less transversely elliptical, but never very markedly so, the horizontal diameter not more than *ca* 20 per cent greater than the vertical one. Scrobicular ring distinct, no other secondary tuberculation, the remainder of the plate being naked. At the adradial edge the plate is unusually narrow, only the scrobicular ring lying between the areole and the margin. On the horizontal margins of the ambital plates only a single series of scrobicular tubercles separates neighbouring areoles; thus contiguous plates each contribute towards forming their commonly shared scrobicular tubercles. The whole admedian border is depressed and naked, forming thus, with the other plates, a zig-zag vertical groove, which is extremely conspicuous.

RADIOLES: Part of the shaft of a single radiole (evidently one of the largest) lies over the apex of the test. It is finely striate, glossy, cylindrical, *ca* 0·5 mm. diameter.

Locality and Horizon

The holotype is merely labelled " Black Head ". In response to an inquiry, Professor W. N. Benson, University of Otago, has kindly sent the following comments (pers. comm. 7/4/1949): " Black Head is presumably the head of that name about three miles south of Dunedin, and if so the horizon of the fossil would be low down in the Caversham Sandstone ". The Caversham Sandstone is of Otaian age (middle Oligocene). The name of the collector is not recorded.

Paratypes

A further specimen of this species, EC 168, in the N.Z. Geological Survey comprises one interamb and the associated ambulacral plates. It comes from the type locality.

A third specimen (in the Geology Department, University of Otago) is larger than the holotype, and more completely exposed, but unfortunately it is somewhat weathered, and does not show the detail of the tuberculation so clearly. It is illustrated in Plates 13, D, and 14, C, since it preserves the general form of the test more naturally than does the holotype. This specimen is labelled " Shag Point ". Professor W. N. Benson comments as follows: " Shag Point is obviously doubtful,

for that point is composed of non-marine coal-measures, though the rocks immediately north of it are marine late Cretaceous, much older than the Caversham Sandstone. On the other hand, the headland immediately south of the Shag River, about a mile or less south of Shag Point, is made of Caversham Sandstone a little higher in that series than the rock at Black Head". The matrix resembles that of the holotype, and so it seems probable that Professor Benson's suggestion is correct, and that the age is Otaian. Late Cretaceous is a quite improbable age for this specimen, which is a well defined *Goniocidaris*, a Tertiary genus. The horizontal diameter of this specimen is 13·0 mm., the height 4·0 mm. It is, however, probably artificially compressed, and the real height would be a little more, perhaps 6·0 mm.

Relationships

Chapman and Cudmore (1928, 1934) have described *Goniocidaris pentaspinosa* from the middle Tertiary of eastern Australia. At the time of their description their species was " distinguished from all other fossil species by the prominent evenly-composed scrobicular ring which has no miliaries visible to the naked eye outside it " (C. & C., 1934, p. 138). In this character, and in its small, depressed test, *G. pentaspinosa* agrees with the present species. Also the ornamentation of the ambulacral plates is similar in both species, the number of coronal plates to the series (seven) in *pentaspinosa* matches that of *pusilla*, and the number of amb plates opposite an ambital coronal plate (six) is the same in both species. It is therefore clear that the two forms must be very closely related.

For the following reasons it seems best to keep the New Zealand form separate from the Australian:

(1) Spines of the Australian species are polygonal in section, bearing five to eight ridges, finely but distinctly serrated. The spine associated with the holotype of *pusilla* has none of these characters.

(2) The ambulacra are straight in the New Zealand form, sinuous in the Australian (somewhat subjective criteria in borderline cases).

(3) The scrobicular rings are not shared in *pentaspinosa*.

These two forms are so closely related that they may prove useful in correlating New Zealand and Australian stages. The topic cannot be fruitfully pursued until the remaining groups of New Zealand Tertiary echinoids have been described, but it is of interest meantime to note that here is a New Zealand Otaian form paralleling an Australian Balcombian species. There are other cases where New Zealand Duntroonian–Waitakian echinoids parallel Australian Janjukian species.

Goniocidaris umbraculum Hutton. (Plates 5, A–G; 9, B; 12, A, E, F; 13, A, B; 14, A)

Cidaris tubaria (Lamarck): Hutton 1872 (NON *Cidarites tubaria* Lamarck, equals *Goniocidaris tubaria*).
Goniocidaris geranioides (Lamarck): Hutton 1887 (NON *Cidarites geranioides* Lamarck, equals *Goniocidaris tubaria*).
Goniocidaris umbraculum Hutton 1879, *Catalogue of the Echinodermata of New Zealand*, p. 10.
Goniocidaris umbraculum Hutton: Mortensen 1928, *Monograph of the Echinoidea*, 1, p. 164.

This species is the only representative of the genus living in New Zealand seas. It is endemic, but is considered by Mortensen and Clark to be related more closely to the Australian species *G. tubaria* than to any other. A full description has been published by Mortensen (1928, p. 164), but no account is available of the structure of the radioles.

Holotype

A naked test, now fragmentary, in the Dominion Museum, Wellington.

The following account, based on material in the writer's collection, refers mainly to skeletal characters likely to be useful in recognizing fragments of the species in Pliocene beds—where it almost certainly will be found.

TEST (Plates 13, A, B; 14, A): Circumference rounded, horizontal diameter up to 26·0 mm. Sides strongly arched, height up to 16·0 mm. Aboral and adoral surfaces somewhat flattened.

AMBULACRA (Plate 5, E): Very weakly sinuate, almost straight, *ca* 30 per cent I.A. Interporiferous zone five times as wide as the poriferous zone. Marginal series of tubercles regular, well separated by intervals nearly equal to their own diameters (not " scarcely contiguous " as Mortensen [1928] states). A small internal tubercle within the marginal tubercle and below it, near the lower suture. In larger specimens, an additional small tubercle below each marginal tubercle, outside the internal tubercle. Internal half of the interporiferous area naked and deeply sunken, forming thus a vertical furrow in the ambulacral midline. Pores circular, the pore-pair obliquely placed, sunken but not conjugate.

INTERAMBULACRA (Plate 5, A): Eight or nine interamb plates to each vertical series. Aboral areoles circular, ambital and subambital ones transversely elliptical, the lowest four or five confluent. Areole deeply sunken near the periphery, the boss rising in a series of rather ill-defined terraces. Sunken peripheral part of the areole with rounded depressions in its floor. Tubercles non-crenulate. Scrobicular tubercles somewhat irregular, reduced along the horizontal sutures. The secondaries are confined mainly to admedian border of the ring, the rest of the admedian area being naked and sunken. Admedian upper and lower borders of plates sunken and naked. Six or seven ambulacral plates opposite each of the larger interambulacral plates.

PRIMARY RADIOLES (Plates 5, B, C, D, F, G; 12, A, E, F): Of varied form, including apical cups, cylindrical tapering forms with paired basal spurs, and transitional types. The microscopic structure of the larger radioles is illustrated in Plate 9, B. The medulla extends about one-third of the way to the periphery. The radial zone is built up of regularly arranged series, each of *ca* 18 perforations. The perforations are square, and so regularly arranged that corresponding perforations of neighbouring series tend to occur opposite one another, resulting in places in concentric arcs of squares. An occasional interpolated series occurs, beginning at some intermediate distance out from the medulla, and having no corresponding end-plate in the cortex. The cortex is deeply ridged, *ca* 12 to 14 ridges, the inner margin of the cortex smooth, because the radial zone does not take part in forming the ridges. The furrows between the ridges are occupied by anastomosing cortical hairs.

In the diagnostic microscopic features the radioles of *Stereocidaris hutchinsoni* are sharply distinguishable from those of *Goniocidaris umbraculum* (cf. Plate 9, B, E). In the former species the radial zone enters into the ridges, in the latter it does not. This is important, since broken fragments of radioles of these two species otherwise look similar; both are likely to occur together in the Nukumaruan stage, though so far only the former species has been recognized.

Distribution

Ranging from Cook Strait to Foveaux Strait, in depths of 40–60 fathoms; not yet known from the west coast of the South Island.

Genus **Ogmocidaris** Mortensen

Mortensen, Th. 1921. *Vidensk. Medd. dansk Naturh. Foren. Kbh. 73*, p. 151.
Type species *Ogmocidaris benhami* Mortensen 1921.

Test low. A well-marked median furrow in both ambulacra and interambulacra. Pores oblique, the wall narrow but distinctly raised, not perforate. Areoles rather deep, sunken, the proximal ones confluent. Tubercles perforate, non-crenulate. Apical system *ca* half the horizontal diameter, or a little more. Peristome a little smaller than the apical system. Primary radioles cylindrical, tapering, twice or three times as long as the horizontal diameter of the test, covered by

short anastomosing hairs, and bearing minute thorns arranged in more or less linear, longitudinal series. Oral primaries flattened, with serrate edges. Scrobicular and upper miliary spines somewhat flattened, the other miliaries cylindrical.

The genus, which is monotypic, is restricted to New Zealand seas, but may be expected in the Pliocene.

Ogmocidaris benhami Mortensen. (Plates 7, F, H; 12, B–D; 13, E, F; 14, B)

Porocidaris elegans Agassiz: Benham 1909 (NON *Porocidaris elegans* Agassiz, equals *Histocidaris elegans*).
Ogmocidaris benhami Mortensen 1921. *Vidensk. Medd. dansk Naturh. Foren. Kbh. 73*, p. 148, Pls. 6, 7.

Holotype

A test with radioles in the Universitetets Zoologiske Museum, Copenhagen.

The following account, based on material in the writer's collection, pays special attention to features likely to be useful in recognizing fossil fragments, should any be found.

TEST: Circumference round, horizontal diameter up to 20·0 mm., height up to 11·0 mm. Flattened above and below, but the apical system may be somewhat tumid (as in Plate 2, B).

AMBULACRA (Plate 7, F, H): Slightly sinuous, *ca* 25 per cent I.A. Interporiferous zone four times the width of the poriferous zone. Marginal series of tubercles regular, sharing the weak sinuation of the ambulacrum, well separated by intervals somewhat less than their own diameters. A prominent internal tubercle, nearly as large as the marginal one, just within and below the marginal, near the lower suture. Additional minute miliaries, usually one just outside the inner tubercle, between the marginals, and another within and above the marginal. Inner (admedian) third of the interporiferous area naked and sunken, except on the aboral plates, forming therefore a conspicuous wavy vertical groove over the ambital and sub-ambital parts of the ambulacrum. Pores circular, obliquely placed, the outer member higher; an outward prolongation of the marginal tubercle forming a prominent ridge along the upper border of the poriferous zone of each plate, so that at first sight the pores seem to be conjugate, though they are well separated by a narrow elevated curved wall, and so are non-conjugate.

INTERAMBULACRA (Plate 7, H): Six or seven plates to the series. All areoles, save the lowermost two or three, circular, occupying almost the whole depth of their plates, the lowest two or three confluent, the remainder with contiguous scrobicular rings. Areoles deeply sunken at their peripheries, the boss not very prominent. Scrobicular tubercles widely separated by intervening spaces which are naked or contain one or two small miliaries. Scrobicular tubercles reduced, and shared in common by neighbouring areoles along their common horizontal sutures. On the admedian zone the miliaries, which are slightly smaller than the scrobicular tubercles, form an arc around the latter; they do not extend to the admedian borders or angles, which remain naked and sunken. Thus there is a conspicuous, but narrow, zig-zag vertical furrow in the midline of each interamb. Six ambulacral plates opposite one ambital coronal plate.

PRIMARY RADIOLES (Text fig. 14, p.28 , and Plate 12, B–D): A typical larger primary radiole measures between 25·0 and 35·0 mm. in length, maximum diameter at the milled ring *ca* 1·5 mm. Shaft a tapering cylinder, usually without ridges, but with more or less linearly arranged minute thorns, their points directed distally. In transverse section (Text fig. 13, p.28) the shaft exhibits a small medulla, the inter-spaces varying from 10 to 30μ across. The radial zone comprises a regular, well-defined region occupying most of the outer two-thirds of the section. Each radial series in an average-sized radiole comprises *ca* 14 perforations, smaller and circular within, larger and transversely rectangular without. The perforations of adjacent series are not opposite one another, or not markedly so. Occasionally a new series is interpolated, beginning near the medulla. Each radial series terminates distally at a prominent end-plate in the cortex. The plates contribute to the thorns, two or three to each. The intervening cortex between thorns is covered by

anastomosing cortical hairs. Fragments of primary radioles are easily distinguishable from all other known Cenozoic species of New Zealand by this characteristic microscopic structure. In living material the collar and milled ring are pink, the rest of the radiole a very pale pink.

Distribution

Apparently restricted to sub-littoral and archibenthic waters along the east coast of the North Island. It has been taken from the following stations:

Off Cape Kidnappers, 200 fathoms, mud, coll. J. A. F. Garrick, 1952, a large specimen in the writer's collection.

Off Opotiki, 70 fathoms, coll. A. W. B. Powell, specimens in the Auckland Museum and the writer's collection.

Off White Island, 55 fathoms, isolated radioles only (Mortensen, 1921, p. 149).

Cape Runaway, 105 fathoms, sand and mud, and Cape Kidnappers, 76–82 fathoms, soft mud, specimens " in considerable numbers " now in the Otago Museum, and two specimens, including the holotype, in the Copenhagen Zoological Museum (Benham, 1909; Mortensen, 1921).

Genus **Notocidaris** Mortensen

Mortensen, Th. 1909. *Echinoidea d. deutschen Suedpolar-Expedition*, p. 17.
Type species *Goniocidaris mortenseni* Koehler.

Test low, rather thin and fragile. Pore zone not distinctly sunken. Pores close together, oblique, separated only by a very narrow, low wall, which may even be perforated, so that the pores become confluent. A naked, somewhat sunken median line in the interambulacra, but not in the ambulacra. No crenulation. Scrobicular tubercles not larger than the other secondaries. Primaries often more or less flattened, the general surface of the shaft with numerous fine, sharp, longitudinal ridges, neck twice the length of collar. Oral primaries spearhead-shaped, usually with coarsely serrate edges. Secondary radioles erect, slender, cylindric, more or less club-shaped, but not flattened. Both large and small globiferous pedicellariae without an end-tooth on valves. No tridentate pedicellariae.

Notocidaris vellai sp. nov. (Plate 15, A–M)

Holotype

Test fragments, associated primary and secondary radioles, and pedicellariae, specimens EC 169–180 in the collection of the N.Z. Geological Survey; GS 4011, Waipuru Shell-bed, Kai-iwi Valley, coll. P. Vella—Nukumaruan (middle Pliocene). In the process of extracting the holotype from the matrix the various elements unavoidably became separated, but they undoubtedly represent a single individual, since all were imbedded in direct contact in a lump of matrix a few centimetres in diameter. All fragments are therefore holotype merotypes. For convenience, they have been allotted separate registration numbers, EC 169–180.

TEST: The dimensions of the fragments imply a small, but robust, somewhat flattened test, horizontal diameter *ca* 25·0 mm., height *ca* 15·0 mm.

AMBULACRA: Slightly sinuate, *ca* 25 per cent of I.A., interporiferous zone just over twice as wide as poriferous zone. Admedian margin of plates neither naked nor sunken, and therefore no median vertical groove in ambulacrum. Marginal series of tubercles regular, the tubercles not contiguous. Either one or two inner tubercles lying adradially to the marginal tubercle on each plate, the inner tubercles forming only one vertical series. Pores close together, the outer pore higher than the inner, the axis of the pore-pair therefore lying obliquely with respect to the horizontal. (NOTE.—Most of the ambulacral plates in the holotype are more or less eroded or completely lacking; the foregoing characters are those of the better preserved plates.)

INTERAMBULACRA: Seven or eight interamb plates to each vertical series (six are actually present in the largest test fragment, EC 179, from which at least one, probably two, adapical plates are missing). Areoles transversely elliptical adorally, becoming circular near the ambitus and above, lying closer to the adradial than to the admedian border, the three proximal areoles confluent, the next two having contiguous scrobicular rings, the uppermost separated from one another. Scrobicules narrow, deep; boss large, prominent, bearing a broad platform and a relatively large hemispherical tubercle. Scrobicular rings ill-defined, scrobicular tubercles similar to neighbouring secondaries. Secondaries arranged irregularly, uneven in size, but smallest along the admedian margins of the tuberculated area. A very narrow, shallow furrow is present along the admedian border of each interamb plate. The following tabulation is derived from two merotype segments, EC 169 and EC 179:

Interamb. Plate	Width (mm.)	Height (mm.)	Width of Areole (mm.)	Number of Amb. Plates Opposite
No. 1 (adapical)		Missing		
No. 2		Missing		
No. 3	7·5	5·0	4·0	9
No. 4 (ambital)	8·5	5·0	4·0	8
No. 5	7·5	4·5	4·0	7
No. 6	5·5	3·0	3·5	6
No. 7	4·5	2·0	2·5	4
No. 8 (adoral)	3·5	1·5	2·0	3

PERISTOME: Not represented, probably *ca* 7 mm. diameter. Some or possibly all of the clubbed cylindrical secondary radioles mentioned below may belong to the peristome.

PRIMARY RADIOLES: Of the twelve primary radioles found with the holotype test fragments, ten have a most distinctive shovel shape or spearhead shape, the shaft flattened and very short, in some cases shorter than the collar. A representative series of types is illustrated on Plate 15, so further description is unnecessary. The radial zone of the stereom is relatively thin, the bulk of the stereom being formed of the medulla. The size and structure of the radioles suggest that they must belong to the adoral plates. The other two radioles in the collection are represented only by their bases and collars, which cannot be distinguished from the corresponding portions of some of the smaller radioles which are supposed to belong to *Stereocidaris hutchinsoni*.

SECONDARY RADIOLES: About fifty of these occur with the holotype, some still attached to their tubercles. Three types are present: (1) flattened scrobicular spines (Plate 15, F); (2) slender, cylindrical or weakly clubbed, cylindrical spines (Plate 15, E); (3) clubbed spines, flattened distally (Plate 15, D). The majority of the specimens found fall in the second class.

PEDICELLARIAE: A globiferous pedicellaria is still attached to a plate of the fragment EC 179, and a further dozen were found by searching the matrix forming the internal mould within the test fragments. All are of the globiferous type, without a terminal end-tooth. The valves vary in size from length 480μ, breadth 170μ, to length 850μ, breadth 350μ, but present no significant differences (Plate 15, B, C, K). No tridentate pedicellariae were found, and it may be assumed that they are absent from the species.

Paratypes

Other matrix from the holotype locality GS 4011 has yielded spade-shaped and spearhead-shaped radioles, interamb plates, and secondary radioles, all of the same kinds as in the holotype. In addition, a few cylindrical fluted primary radioles were found, similar to the smaller primaries of *Stereocidaris hutchinsoni*. As the latter occurs in the Nukumaruan, it is uncertain whether these cylindrical radioles belong to *N. vellai*. A spade-shaped radiole was found in matrix from GS 5438 (upper Nukumaruan), and other fragments from GS 4204 (lower Nukumaruan) seem to belong to *N. vellai*.

Stratigraphical Range

Lower and upper Nukumaruan (middle Pliocene).

Systematic Position

Despite the unusual wealth of microscopic structures present in the holotype, the genus to which this species should be referred remains problematic, largely because it is not yet clear whether the smaller cylindrical radioles which have been referred to *Stereocidaris hutchinsoni* really belong to *Notocidaris vellai*. In seeking the generic position of each of the two species, therefore, only those structures known with certainty from each may be considered. Reasons for referring *hutchinsoni* to the genus *Stereocidaris* have been given under that species (p. 36).

The large and small globiferous pedicellariae which lack end-teeth, the non-conjugate pores, and the absence of a naked, median, ambulacral groove or depressed ambulacral sutures are characters of *vellai* which eliminate all Cidarid genera except *Stereocidaris* and the Ctenocidarina. The close-set, slightly oblique pores and the confluent lower areoles point to the Ctenocidarina, where these characters are usual. Within the latter grouping, the genus *Notocidaris* is distinguished by having spearhead-shaped oral radioles; indeed, no other genus of Cidaridae is known to have oral radioles of this type. On the other hand, living species of *Notocidaris* are not known to have flattened scrobicular radioles; but since the closely related genus *Ctenocidaris* does possess them, undue weight should not be placed on that apparent discrepancy. There are other discordant features, however; the robust character of the interamb plates of *vellai* contrasts with Mortensen's (1951) description of the test of *Notocidaris* as " rather thin and fragile ". Again, if the cylindrical fluted radioles occurring at the holotype locality GS 4011 can be proved to belong to *vellai*, that species will differ still more from known species of *Notocidaris*. Should future investigations show that all the Cidarid structures found at the type locality belong to a single species, it may be preferable to erect a new genus to accommodate it. Meantime, the balance of evidence favours referring *vellai* to *Notocidaris*.

Since the above comments were written I have had the opportunity of examining the *Notocidaris* material in the University Zoological Museum, Copenhagen. In the species *Notocidaris remigera* Mortensen the larger scrobicular radioles are in fact flattened, a feature not mentioned by Mortensen (1950). Specimens of *Notocidaris gaussensis* are by no means " thin and fragile ". Thus, these two characters vary according to the species, and are not of generic value. It is therefore concluded that *Notocidaris vellai* is correctly placed in the genus *Notocidaris*. To Dr P. L. Kramp and Mr F. Jensenius Madsen I am indebted for their kindness in placing the Copenhagen University collection at my disposal.

Nukumaruan Sea Temperatures

In view of the uncertainty over the generic placing of *N. vellai*, the species was not discussed in the section on Tertiary climates in this bulletin. It should be noted here, however, that if the generic placing can be confirmed it will support Fleming's (1944) suggestion that there was a lower Nukumaruan incursion of cool-water forms from the south. *N. vellai*, however, does not seem to have been markedly stenothermal, since it survived into the upper Nukumaruan, which Fleming considers to have been not much cooler than present-day seas.

Genus **Eucidaris** Pomel

Pomel, A. 1883. *Classification méthodique et genera des Echinides vivants et fossiles, p. 109.*
Type species *Cidarites metularia* Lamarck.

Pores non-conjugate. Primary radioles typically cylindrical, terminating in a small crown with a central prominence, the shaft with low rounded warts arranged in rather distinct longitudinal series. Alternatively the radioles may be fusiform, or very thick and club-shaped.

Mortensen (1928) considers that the terminal crown of the radioles, with a central prominence, constitutes the main diagnostic character of the genus.

The lower Tertiary beds of New Zealand contain a variety of radioles referable to *Eucidaris*. Most of the forms intergrade, and at present it is possible to distinguish only two well-marked species.

KEY TO THE NEW ZEALAND SPECIES

Shaft of primary radiole widening abruptly to about three times its initial diameter, and then tapering abruptly to the apex, bearing very deep longitudinal fossae and ridges .. .. *coralloides.*

Shaft of primary radiole fusiform. Sculpture comprising prominent, rounded warts arranged in longitudinal series .. .. *strobilata.*

Eucidaris coralloides sp. nov. (Plate 11, B, C)

Holotype (Plate 11, B, C)

A primary radiole, lacking the base and collar, EC 154 in the N.Z. Geological Survey collection; GS 5516, Allday Bay, base of Campbell's Beach limestone, coll. J. Marwick. Whaingaroan (basal Oligocene).

PRIMARY RADIOLE: Length 19·0 mm., major diameter 13·0 mm., diameter of terminal prominence 1·5 mm. The shaft is excavated into *ca* ten longitudinal fossae, separated by as many longitudinal ridges, whose distal parts unite to form the crown. Nearer the base of the shaft a number of subsidiary ridges occupy the lower parts of the depressions between the ridges. The lower quarter of the shaft has a diameter of *ca* 4·0 mm. and carries a few warts or thorns. About 5 mm. above the broken lower edge the diameter of the shaft abruptly widens to *ca* 13·0 mm. diameter, thereafter tapering towards the apex.

The extraordinary shape of the radiole enables the species to be distinguished from all other Cidarids at a glance. The prominent apical crown and central tubercle confirm the generic position. The only Cidarids at all comparable with this are the Mesozoic *Tylocidaris* and *Balanocidaris*, both with massive clubbed spines, but lacking the deep excavations and the terminal crown and prominence. This species, unique in *Eucidaris* in the exaggerated clubbed form of the radiole, supports Mortensen's (1928) suggestion that *Balanocidaris* and *Tylocidaris* are related to *Eucidaris*. The species does not appear to be closely related to any other species of *Eucidaris*, but until we know the characters of the test it would be unwise to relegate it to a distinct genus of its own.

Cidarid Coronal Plates incertae sedis

The ambital and subambital plates of the interamb of a cidarid EC 125, from the type locality of *Eucidaris coralloides* (GS 5516), may possibly belong to that species. The dimensions of the ambital plates suggest that the test would have a horizontal diameter of *ca* 30·0 mm., and a height of *ca* 11·0 to 14·0 mm. The interambulacral ambital plates have a breadth of 8·5 mm. and a height of 5·0 mm. Only four interamb plates of each series are preserved. The total for each column probably would be about eight. An ambital plate is illustrated in Text figs 10 and 11, p. 28. Scrobicular rings complete, but broadly contiguous along the horizontal sutures. Scrobicular tubercles large, prominent, widely separated by one, two, or three small intervening miliaries. Scrobicular tubercles reduced in size along the horizontal sutures, where only a single, shared series occurs. Areoles large, occupying almost the whole depth of each plate, situated nearer the adradial margin than the admedian margin, circular on the subambital plates, slightly elongate transversely at the ambitus. The undulating adradial margins of the plates indicate a sinuous ambulacrum. The broad admedian zone is fully covered by secondary tubercles. The median vertical sutures are distinct, but not sunken. Bosses and tubercles very prominent, non-crenulate.

The general appearance is reminiscent of *Eucidaris tribuloides*, particularly because of the prominent, raised bosses and the broad admedian miliary zone with distinct vertical suture-line. Until the associated radioles are known there can be no certainty as to the generic position.

Eucidaris strobilata sp. nov. (Plates 8, A, E, F, G, H, J; 10, B; 11, E)

Holotype (Plate 8, E, J)

A primary radiole, EC 129 in the N.Z. Geological Survey Collection; GS 1179, Red Bluff, Chatham Island, coll. J. Marwick, 1924. Age uncertain, probably about lower Oligocene or upper Eocene.

PRIMARY RADIOLE: Total length 22·0 mm., height of base 1·0 mm., height of collar 3·0 mm., height of neck 1·0 mm., length of shaft 16·0 mm., height of central prominence 1·0 mm. Width of base *ca* 2·0 mm., width of neck 3·0 mm., width of mid-shaft 5·0 mm., width of crown 4·0 mm., width of central prominence 1·5 mm.

General shape fusiform, with an abrupt terminal truncation. Shaft carrying rounded, rather prominent warts, larger on one side than on the other, arranged in longitudinal series, the warts in neighbouring rows alternating so as to produce a series of intersecting spirals, in the same way that the scales on a pine-cone form both longitudinal and intersecting spiral series. Terminal crown of 12 radial ridges, surrounding the central prominence, which itself bears about seven warts.

Paratypes

The holotype was selected as showing the greatest number of characters. It is, however, by no means the largest specimen. Similar radioles from the type locality range up to 33·0 mm. in length, and up to 8·0 mm. in diameter of shaft.

Some spines from the type locality show varying degrees of loss of warts, whilst the shaft becomes invested by a white enamel-like coat. In extreme cases the whole spine is reduced in size and takes on the appearance of a mammalian incisor (see Plate 8, F). A third type of spine, now in the Dominion Museum, labelled Chatham Islands, probably comes from the same locality (it is accompanied by a spine of the typical form). It has the warts arranged in much more regular longitudinal series, with little trace of the spiral series, the warts also being much smaller, though the spine is of average size (length 23 mm.). Spines of a fourth kind (Plate 8, A) resemble the Dominion Museum specimen, but are much smaller, only 7·0 mm. in length. These taper distally, and consequently have the terminal crown much reduced. A fifth type of spine (Plate 8, G, H) shows the development of longitudinal ridges on the distal part of the shaft, the ridges merging with the longitudinal rows of warts. Radioles of type four and type five occur together at locality GS 3600. Bearing in mind the considerable differences between the individual radioles on a specimen of the Recent *Eucidaris thouarsii*, for example, it would seem probable that all the above types are to be referred to the one species. The smaller radioles would be oral primaries, the larger, robust ones would be ambital and neighbouring radioles, whilst the " tooth-like spines " must remain something of a mystery. The similarity of the proportions of base, collar, and neck, as well as the existence of intermediate types, indicates that the tooth-like forms belong to the same series as the other large types; possibly they are adapical radioles, modified to an extreme degree just as *Goniocidaris* has excessively modified adapical " cups ".

A transverse section through the shaft of a radiole of the typical form (Plate 11, E) shows that the thickness is chiefly due to a greatly developed radial zone. The medulla is relatively restricted, occupying only about one-fifth of the radius. The outer cortex varies considerably in thickness, and carried a hairy covering, most of which has been lost in the fossils. Traces are seen in the depressions between the warts, and in occasional cortical processes projecting beyond the surface. The warts themselves are formed of radial zone, covered by cortex. The radial series are very regular, interpolated series commencing at all distances out, to provide for the increasing circumference. Each interpolated series begins with a sequence of very small, gradually increasing perforations.

Spines of type four have an entirely different transverse section, with the cortex alone producing the warts, the radial zone remaining of constant radius (Plate 10, B). Only *ca* 17 perforations occur in each radial series, and as the rays do not increase in number by interpolation, the perforations widen distally to accommodate the increasing circumference. Thus they are circular within, transversely oval without. The cortical end-plates are large, always deeper than broad, extremely deep in the warts. No cortical hairs or meshwork survive.

Despite the great structural differences between these two types of spine (that is, between the type exemplified by the holotype, and the so-called fourth type), the existence of an intermediate kind (type three) suggests that all belong to one species. As there is only one specimen of the intermediate third type, it is not desirable to section it in order to discover its microscopic structure. This must await more material. But if all are correctly assigned to the one species, a transitional form may be expected in which the warts are made up of both radial and cortical stereom. The external aspect of the " tooth-like " spines suggests that it is here again the cortex that is greatly developed, and responsible for the enamel-like appearance of the surface but the few specimens ought not to be sacrificed for sectioning at this stage.

Localities

GS 1179: Red Bluff, limestone, Chatham Islands, holotype and paratype radioles of first and second types in the collection of the New Zealand Geological Survey, EC 129, 131, 155. Also radioles of the first and third type in the Dominion Museum. Age probably either upper Eocene or lower Oligocene—about Runangan–Whaingaroan.

GS 3600: Lindhurst Survey District, Mataura River, $4\frac{1}{2}$ miles down stream from Mataura Bridge, radioles of the fourth and fifth type, coll. R. W. Willett, 1945, in the collection of the N.Z. Geological Survey, EC 128, 130. Waitakian.

GS 486: Wharekuri Greensand, Wharekuri, Waitaki Valley, Otago, a fragment of a radiole apparently of the first (holotype) variety, but with more numerous and more thorny warts, coll. A. McKay, 1880; in the collection of the N.Z. Geological Survey, EC 153. Duntroonian.

Stratigraphical Range

Upper Eocene or basal Oligocene to Waitakian (middle Oligocene).

Relationships

To judge from the illustrations given by Chapman and Cudmore (1934, Plate XIV, Figs 25, 26), their unnamed spines (" Club-shaped spines, *incertae sedis* ") must have belonged to a related species. They are more markedly fusiform than spines of the present species, taper to a sharper termination, and clearly represent a distinct species. Chapman and Cudmore evidently suspected that their material might be *Eucidaris*, but did not publish anything further. H. L. Clark (1945) seemed to think these radioles were referable to *Phyllacanthus*, but the presence of what appears (from Chapman and Cudmore's illustrations) to be a terminal crown and prominence, and the general Eucidarid look of the radioles, hardly supports such a view. The question, however, is one for future investigation.

Genus **Phyllacanthus** Brandt

Brandt, I. F. 1835. *Prodromus descriptionis animalium*, p. 67.
Type species *Cidarites (Phyllacanthus) dubia* Brandt.

Test thick, with prominent non-crenulate tubercles. Scrobicular tubercles conspicuous, usually with a well-limited elevation on the side towards the areole. Ambulacra sinuate. Pores conjugate, but with the upper part of the wall between them somewhat raised. Marginal tubercles

prominent, the internal tubercles crowded, smaller than the marginal ones, and more numerous than the latter. Primary radioles thick and stout, cylindrical or fusiform, with fine granules more or less distinctly arranged in series, on the whole smooth, without prominent thorns. Radial laminae of the primary radioles, as seen in transverse section, arising in fan-like bundles from radial projections of the inner medulla. Secondary spines broad, flat, closely adpressed, the minor ones scale-like.

KEY TO THE NEW ZEALAND SPECIES

Interambulacral midzone at the ambitus as broad as the largest areoles. Ambital areoles near the admedian border of their plates .. .. *wellmanae.*

Interambulacral midzone at the ambitus no more than half as broad as the largest areoles. Ambital areoles about equidistant between the admedian and adradial borders of their plates .. .. *titan.*

Phyllacanthus titan sp. nov. (Plates 1, B; 3; 10, A; 11, D)

Holotype (Plates 3, G; 11, D)

The proximal half of a primary radiole, EC 105 in the collection of the New Zealand Geological Survey; GS 172, Hutchinson's Quarry, coll. A. McKay, 1876—Hutchinsonian (upper Oligocene).

PRIMARY RADIOLE: Length of type fragment 81·0 mm.; the tapering (which paratypes show to be fairly even) indicates an original total length of the order of 160·0 mm. Diameter at base 4·0 mm. Diameter at milled ring 7·0 mm. Diameter at top of collar 6·0 mm., and at top of neck 6·0 mm. Height of collar 2·0 mm. and of neck 2·5 mm. Maximum diameter of shaft (about 10·0 mm. above the top of the neck) 8·0 mm. Diameter of shaft at distal broken end 6·0 mm. Sculpture: Milled ring vertically striate, *ca* 7 or 8 striae to 1 mm. Collar vertically striate, more finely so than the ring, *ca* 14 to 16 striae to 1 mm. Shaft with an outer and an inner cortex. Outer cortex finely granulated. On the holotype the inner cortex is exposed near the base of the shaft, and can be seen to be coarsely and regularly granulated, the granules rounded, each *ca* 0·3 mm. diameter, arranged in regular longitudinal rows (Plate 11, D).

Paratypes

More than two hundred primary radioles referable to this species have been collected from the type locality. The majority (including the holotype itself) were secured by Alexander McKay in 1876, and now form a notable series in the N.Z. Geological Survey Collection.

Phyllacanthus titan is apparently the largest Cidarid known from the Australasian area. The massive spines considerably exceed those of *Phyllacanthus imperialis* and the more slender spines of *P. longispinus*. The holotype has been selected as the specimen showing the greatest number of diagnostic features, and is by no means the largest. More massive must have been the spine of which the base is illustrated in Plate 3, C. Its milled ring measures 10·0 mm. in diameter. It seems likely that the total length of the largest primaries must have reached 200·0 mm. (compared with 74·0 mm. for *P. imperialis* and 80·0 mm. for the largest slender spines of *P. longispinus*).

As in the living species of the genus, the longitudinal series of granules become more and more pronounced towards the extremity of the shaft, and near the apex itself fuse into longitudinal, prominent ridges, separated by deep flutings (Plate 3, A, H). The smaller primaries show longitudinal flutings and ridges over most, or all, of the shaft. Some variability in this regard is also seen in the larger radioles, of which there are examples with very prominent rows of contiguous granules not obscured by the thin overlying outer cortex.

In transverse section the radiole is typical of *Phyllacanthus* (Plate 10, A, D). The medulla is restricted to the innermost region, and extends outwards as rays into the base of the radial zone, thus separating the lamellae into clusters of varying size. Owing to secondary crystallization it is

frequently difficult to distinguish the minute detail of these clusters. In uncrystallized specimens, however, the inner radial fans of the clusters of lamellae can be distinguished, structures diagnostic of *Phyllacanthus*. Even in the broken ends of such specimens the fans can be seen clearly, as for example in the radiole from GS 3600 (Plates 3, A; 10, D). Over most of the shaft the inner cortex is about as thick as the outer (Plate 10, A), but near the end of the radiole, where the ridges and flutings are prominent, the inner cortex is much thicker than the outer, and by its varying thickness is responsible for producing the ridges (Plate 10, D). In fluted radioles there are as many cortical ridges as there are medullary rays and radial fans. The medullary rays lie opposite the cortical ridges, whilst the radial fans, which alternate with the medullary rays, consequently lie opposite the cortical flutings.

It would appear, from the material examined, that the earlier forms (Duntroonian and Waitakian) have a more pronounced granulation of the cortex than do the later ones from the Hutchinsonian. Whether this represents a constant, or specific, distinction is as yet uncertain.

TEST: No specimens have as yet been found in which portions of the test are directly associated with radioles. There are no test fragments at all in collections from the type locality. However, in collections from the Weka Pass and from Curiosity Shop in the Rakaia Valley there are *Phyllacanthus* plates, including some of size corresponding to the largest of the radioles. These plates occur together with radioles of *Phyllacanthus titan*, though there are no specimens in which a spine is directly attached to a plate. Only one species of *Phyllacanthus* seems to be represented by the plates, which therefore are all referred to *Phyllacanthus titan*.

INTERAMBULACRA: A fragment of an interamb plate from locality GS 311 (specimen EC 157) bears a tubercle 4·0 mm. in diameter. It fits the acetabulum of the largest available radiole, the paratype EC 102 (Plate 3, C) with the 10·0 mm. milled ring. It clearly could not belong to any other species of Cidarid yet known from the New Zealand lower Tertiary. The plate fragment, 4·0 mm. thick below the tubercle, indicates an extremely massive test. Working downwards from this large fragment through the smaller plates, all can be grouped into one series. The better preserved specimens show the inner and outer elevations of the scrobicular tubercles, diagnostic of *Phyllacanthus* (e.g., EC 147). In some specimens there is a broad upper zone covered by secondaries (Plate 3, E); in others the areoles are contiguous but not confluent and the scrobicular ring therefore remains complete. The shape of the areole varies from circular to transversely oval, but even in the latter case both the median and outer areas remain broad and well covered by secondary tubercles. The median borders of the interamb plates are depressed, forming a zigzag sunken suture line on one test fragment. Nowhere, however, is this suture line naked. Opposite large plates 20 ambulacral plates occur (Plate 3, E). This unusually large number reflects the relatively great height of some—evidently the supra-ambital—plates.

AMBULACRA (Plate 3, D): Some complete interambulacral plates have attached ambulacrals. The ambulacra were evidently sinuate. The pores are conjugate, but not strongly so. On each ambulacral plate the interporiferous area is equal in width to the pore-zone, which indicates that the complete interporiferous area of the ambulacrum as a whole was twice as wide as a pore-zone. The marginal series of tubercles is distinct, regular, the tubercles contiguous. The inner tubercles are smaller, crowded, irregular. The whole interporiferous area is well raised above the level of the poriferous zones, as in Recent species of the genus.

Localities

GS 172: Hutchinson's Quarry, Oamaru, coll. Alexander McKay, 1876. Holotype EC 105 (primary radiole) in the N.Z. Geological Survey Collection; also 202 primary radioles, including figured paratypes, in the same collection. Five primary radioles from the same locality in the Geology Department, University of Otago, and fourteen primary radioles in the Dominion Museum, Wellington. Hutchinsonian.

GS 74: Curiosity Shop, Rakaia River, Canterbury, coll. A. McKay, 1879. Two interamb plates and two primary radioles in Canterbury Museum, Christchurch. Ten primary radioles (some showing strong surface granulation) and 25 interamb plates, including a figured paratype, in the N.Z. Geological Survey Collection. Two unlabelled interamb plates in the Geology Department, Otago University, are probably from the Curiosity Shop.

GS 2225: Burnside Marl Pit greensand, an eroded radiole fragment, EC 164, coll. M. Ongley—Waitakian.

GS 3600: Mataura River, apex of primary radiole, EC 100 (Plate 3, A)—Waitakian.

GS 5753: Site of old kiln on Karetu River, Whiterock Limestone, Mount Grey Survey District, 3 radioles, coll. B. H. Mason, EC 158—Duntroonian–Waitakian.

A fragment of test, comprising parts of six ambital and subambital interambulacral plates, and a few ambulacral plates, from the uppermost Mount Brown beds, zone F, Weka Pass, coll. J. A. Thomson, are probably referable to this species. The ambulacra (Plate 1, B) are closely comparable with *P. titan*. The interambulacral mid-zone, however, is somewhat broader than in the Oligocene forms, and shows some similarity to *P. wellmanae*. This specimen, EC 104 in the N.Z. Geological Survey collection, is of Waiauan (middle Miocene) age. It is perhaps an intermediate form between typical *P. titan* of the Oligocene and *P. wellmanae* of the upper Miocene.

Relationships

P. titan does not seem to have any closer relative than *P. wellmanae* (p. 51), to which, however, the relationship is no closer than can be inferred from the remarks in the preceding paragraph. See also under *P. wellmanae*.

Stratigraphical Range

Duntroonian to Waiauan (lower Oligocene to middle Miocene). The species is as yet known only from Duntroonian, Waitakian, Hutchinsonian, and Waiauan stages. It is particularly prominent in Hutchinsonian collections. It is possible that future collections will show that the three forms mentioned above are of more limited time range, and in such case it may be possible to break the species up into more convenient smaller sections. This, however, cannot be justified on our present collections.

Phyllacanthus wellmanae sp. nov. (Plates 1, C, D; 2)

Holotype

Portion of a test, EC 167 in the collection of the N.Z. Geological Survey; GS 5832, N62/506, small hill two-thirds of way along first sandy beach south of Cape Runaway, coll. Mrs H. W. Wellman, January 1953—Kapitean (uppermost Miocene).

TEST: Circumference rounded, h.d. *ca* 75·0 mm., height *ca* 55·0 mm. Apical system *ca* 20·0 mm. diameter. The apex is lacking, but its dimensions are evident from the vacant space left.

AMBULACRA: Sinuate, *ca* 12 per cent I.A. Interporiferous zone equal in width to poriferous zone. Marginal series of tubercles regular, almost contiguous. A smaller internal tubercle within and slightly below the marginal. Pores transversely elliptical, lying within a shallow, transverse depression, separated from each other by an interval equal to the width of one of them. Intervening wall broken by a shallow groove along the lower margin, so that the pores are conjugate. The upper margin of the plate is ridged where it traverses the poriferous zone, so that neighbouring pore pairs are separated by transverse raised bars. The whole poriferous zone lies at a lower level than the interporiferous zone.

INTERAMBULACRA: Nine interamb plates to each vertical series. The uppermost areole of each series is circular, the remainder are transversely elliptical. Except for the rudimentary adapical plate, the scrobicular rings merge on all the plates above the ambitus, and the areoles are confluent on the five subambital plates. The scrobicules are shallow, the boss large and prominent, rising to form a broad platform, which bears the hemispherical tubercle. Scrobicular tubercles separated by intervals which are occupied by one or two secondary tubercles. The secondaries are confined mainly to the median zone, which occupies about one-quarter of the whole interamb. The secondaries here form more or less transverse series, of up to 9 or 10 tubercles at the ambitus, fewer elsewhere. A few secondaries occur also on the outer border of the plates, but none occur between the scrobicular rings. The ambital interambulacral plates correspond to 15 ambulacral plates, and measure on the holotype 23·0 mm. by 11·0 mm. However, the highest plates occur between the ambitus and the apical region. The second from the apical region measures in the holotype 16·0 mm. wide by 12·0 mm. high, and it is adjacent to 17 ambulacral plates. Admedian suture not visible, though the midline is depressed.

The subambital region is too imperfectly preserved in respect of its surface sculpture to warrant figuring, but, instead, the following tabulation over one complete interamb column may be given:

Interamb. Plate	Width (mm.)	Height (mm.)	Width of Areole (mm.)	Number of Amb. Plates Opposite
No. 1 (adapical)	8	7·5	4	8
No. 2	16	12·0	6	17
No. 3	21	11·0	13	16
No. 4 (ambital)	23	11·0	14	15
No. 5	23	11·0	14	*ca* 13
No. 6	20	9·5	15	? 12
No. 7	16	8·5	12	*ca* 12
No. 8	*ca* 11	6·0	8	?
No. 9 (adoral)	*ca* 6	*ca* 3·0	*ca* 4	?

PERISTOME: Probably about 30·0 mm. across.

No other material has yet been found, and the radioles are unknown.

Relationships

It is evident that this species is extremely closely related to the Australian Tertiary form *Phyllacanthus duncani* Chapman and Cudmore. Indeed, it may prove to be no more than a local variety. The most striking characteristic the two forms have in common, separating them from all other known species of *Phyllacanthus*, is the broad interambulacral mid-zone. The ambulacral plates are variable in *P. duncani*, according to Chapman and Cudmore (1934), but one of the forms they list corresponds to that found in the holotype of *P. wellmanae*. *P. duncani* occurs in the Janjukian, Balcombian, and Kalimnan of Australia. Tempting as it is to consider the New Zealand species as identical with the Australian, the following considerations seem to make such a course impossible at present. In all hitherto-known species of *Phyllacanthus* there are never more than two confluent areoles (in the lowest plates). According to Chapman and Cudmore, none of the areoles are confluent in *P. duncani*, though the scrobicular rings merge on the lower plates. In *P. wellmanae* the confluence of the areoles on the five subambital plates sets the form apart from all others. Further, the disposition of the ambulacra in relation to the interamb plates differs in the Australian and New Zealand forms. In the latter it is the supra-ambital plates which are highest, and which have most ambulacrals opposite them. According to Chapman and Cudmore there are probably only 7 interamb plates to the series in *P. duncani*, as against 9 in the New Zealand form. This would

account for the more pronounced transverse elongation of the areoles in *P. wellmanae*. Thus, when the known limits of variation in living species are considered, *P. wellmanae* can scarcely be referred to *P. duncani*, unless the holotype is an abnormal or senile form. Since the senile form of *P. duncani* reported by Chapman and Cudmore from Port Macdonnell has four rows of tubercles on the ambulacral plates (as against two or three on normal specimens), the New Zealand form would hardly be referable to a mere senile variant.

Nevertheless, the close relationship between the two species is undeniable, and they may prove to be contemporary equivalents on either side of the Tasman. The persistence of the Australian species into the lower Pliocene (Kalimnan) is explicable by supposing that the south-east Australian climate was still warm at that time, whereas the New Zealand climate may have cooled at the close of the Miocene.

Evolution

The earlier species, *P. titan*, differs from *P. wellmanae*, from *P. duncani*, and from living species in its less markedly conjugate pores. It seems likely that *P. titan* is related to some more generalized non-conjugate ancestor, from which the Phyllacanthids descend. It is interesting to note that the typically Phyllacanthid radiole had already developed before the test characters had taken on the modern characteristics in full. The scrobicular tubercles in *P. titan* exhibit the Phyllacanthid form—those of the holotype of *P. wellmanae* are too poorly preserved to indicate their nature.

Genus **Prionocidaris** A. Agassiz

Agassiz, A. 1863. *Bull. Mus. Comp. Zool. 2*, p. 18.
Type species *Cidarites pistillaris* Lamarck.

Test rather thin and fragile. Primary tubercles non-crenulate, or at most only faintly crenulate. Pores usually distinctly conjugate. Peristome slightly smaller than the apical system. Primary radioles rather slender, mostly tapering, often widened at the point, more rarely simple and cylindrical, as a rule coarsely thorny, the thorns forming more or less distinct longitudinal series, but sometimes arranged in more or less distinct whorls. Collar not usually very long.

Two classes of radioles, from the New Zealand Eocene and Oligocene respectively, seem to be referable to this genus. Until portions of the test are available, however, there can be no certainty that they belong to this genus, or any other. One group of radioles, from the Oligocene (Duntroonian to Otaian), is regarded as corresponding to one species. They are referred to *Prionocidaris* because of their rather close resemblance to radioles which, as Chapman and Cudmore (1934 p. 134) were able to show, belong to *Prionocidaris scoparia*, of the lower and middle Tertiary of Australia. The other group, from the Bortonian Stage of New Zealand, constitute evidence of a second species, which is referred to *Prionocidaris* because there does not seem to be any other genus to accommodate them. They do not accord well with our present conception of *Prionocidaris* and may perhaps represent a new genus ; the point, however, cannot be determined on evidence of the radioles alone. Neither species should be regarded as reliable evidence that *Prionocidaris* occurs in the New Zealand Tertiary until fuller proof is forthcoming, and neither has been cited in the general section of the present work. On the other hand, both species show quite distinctive *specific* characters, and are therefore available for use as index fossils in stratigraphy, should their range be demonstrably limited.

Key to the New Zealand Species

Radioles cylindrical, with a glossy surface, having coarse thorns forming longitudinal series. Collar about twice as long as the diameter of the shaft .. .. *marshalli.*

Radioles cylindrical proximally, flattened distally. Thorns scattered over the proximal two-thirds of the shaft, not in distinct longitudinal series. Collar about as long as the diameter of the shaft .. .. *haasti.*

Prionocidaris marshalli sp. nov. (Plates 8, B, C, I; 9, C)

Holotype (Plate 8, I)

A primary radiole, lacking the distal extremity of the shaft, EC 133 in the collection of the N.Z. Geological Survey; Hampden beds, Hampden Beach, coll. P. Marshall,—Bortonian (middle Eocene).

PRIMARY RADIOLE: Length of fragment 40·0 mm. Width of base *ca* 2·0 mm., width of milled ring 3·5 mm., width of neck and of shaft 2·5 mm., height of base *ca* 2·0 mm., height of collar 5·0 mm. The neck and collar are both finely striate, as is usual in Cidaridae, but the whole shaft is peculiar in being also striate. This results from the remarkably thin cortex (see below), which is glossy and translucent, and reveals the longitudinal lamellae below it. One side of the shaft carries scattered, small thorns. The band of small thorns is delimited on either margin by a left and right longitudinal series of very coarse thorns. Most of the latter are broken in the holotype, but the few complete ones show that the distal extremity of each thorn points towards the distal extremity of the radiole (a feature confirmed by the paratypes). The whole shaft and the neck is glossy, almost pearly, in appearance, contrasting with the collar, which is darker in colour, and matt in texture.

Paratypes

Other material from the type locality (Plate 8, B, C) includes a paratype EC 134 with extremely coarse thorns, arranged in two longitudinal series, one on either side of the shaft, the diameter of the shaft being 3·5 mm. The thorns are more irregularly arranged in a second paratype EC 135, with shaft diameter 2·5 mm.

The cross-section of the shaft (Plate 9, C) is more or less circular, distorted by the presence of the thorns. It is characterized by the extremely narrow cortical zone, the central medulla and the radial zone together making up nearly the whole of the stereom. In the radial zones there are *ca* 30 perforations to the series, the perforations smaller and nearly circular near the medulla, becoming transversely elongated, and somewhat rectangular towards the cortex. No detail is discernible in or on the cortex, but its smooth, glossy external surface indicates that it probably did not carry hairs.

Systematic Position

Of Goniocidarids with thorny primary radioles there does not seem to be any species which approximates to this form. The collar is always short in *Goniocidaris*, and usually there is some indication of a basal disc. Also, we know that lower Tertiary species had a thick cortex, like that of Recent species. *Chondrocidaris* may have a long collar, and this genus shares with the present form a very thin cortex. On the other hand, radioles of *Chondrocidaris* have an entirely different surface sculpture from that of the present species, the thorns being longitudinally flattened into flange-like structures which merge into narrow, deep ridges over the distal part of the shaft. Also *Chondrocidaris* has an irregular system of lamellae in the shaft which, accordingly, is not striate. Lastly, *Chondrocidaris* radioles are usually more massive, relatively thicker, than these.

Prionocidaris includes some living species with similar thorns arranged in much the same way as here—for example, *P. bispinosa*. But the collar is usually short in *Prionocidaris;* however, there is a Recent form, *P. baculosa longicollis*, in which the collar is as long as in the present species. The cortex is not, so far as I am aware, thin in Recent species of *Prionocidaris;* no information appears to have been published as to the internal structure of the radioles of fossil species.

Prionocidaris haasti sp. nov. (Plates 10, C; 11, F–H)

Holotype (Plate 11, F)

A primary radiole, lacking the distal extremity of the shaft, EC 161 in the collection of the N.Z. Geological Survey; Weka Pass Stone, " middle Waipara, opposite McKay's " (an old label).—Duntroonian–Waitakian (Oligocene).

PRIMARY RADIOLE: Total length of type fragment 58·0 mm. Width of base *ca* 2·0 mm., width of milled ring apparently *ca* 3·5 mm. (it is eroded), width of neck *ca* 2·5 mm., diameter of shaft 2·5 mm. Height of base 2·0 mm., height of collar 2·5 mm., height of neck 2·5 mm. The shaft is irregularly beset with rather small, though prominent, thorns, unevenly scattered.

Paratypes

Other material of the species is available from the type locality, and includes a radiole EC 161/A (Plate 11, G) with a complete shaft, lying in the same matrix as the holotype. The shaft tapers to a point distally, at the same time becoming flattened. Total length of radiole 58·0 mm. Other fragments from the Weka Pass indicate that the diameter of the shaft may reach 3·5 mm., and the length, if proportionately the same, would thus be about 80·0 mm. A fragment which indicates a size intermediate between the extremes just given comes from the Curiosity Shop beds, of the same age as the Weka Pass.

The cross-section of the shaft (Plate 10, C), taken at a point where the distal flattening is developed, indicates that the medulla and radial zones make up virtually the whole of the stereom, the cortex forming only a narrow limiting layer over the outside. Thus there are points in common with *P. marshalli*. The irregular shape of the spine is reflected in corresponding irregularities in the length and arrangement of the radial lamellae. Interpolated lamellae are frequent. The perforations are circular, larger towards the periphery. The structure of the narrow cortex is difficult to discern, but, as in *P. marshalli*, it is of even thickness. The thorns are produced by variations in the radial zone, which the cortex envelops, not by variations in the cortex itself.

Localities.

WEKA PASS Stone, Weka Pass, radioles and fragments, including the holotype, in the collection of the N.Z. Geological Survey. Duntroonian–Waitakian.

CURIOSITY SHOP, Rakaia Valley, a fragment of a radiole in the Canterbury Museum, probably collected by Sir Julius von Haast—Duntroonian–Waitakian.

GS 5667: Old Rifle Butts, Oamaru, portion of radiole, EC 162 (Plate 11, H), coll. M. Gage—Otaian.

Stratigraphical Range

Duntroonian to Otaian, Oligocene.

Relationships

These radioles are very similar to those of *Prionocidaris scoparia* Chapman and Cudmore (1934). The resemblance is particularly marked in the case of the shaft-fragment EC 162, from GS 5667. This specimen, like the Australian form, has a fine granulation between the thorns. However, the lack of a flared apex in paratype EC 161/A, and the more acute termination of its shaft, as well as the lack of any test material, makes it advisable to keep the two forms separate, at least for the present.

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PLATE 1

The major dimension is given for the portion illustrated in each case.

Stereocidaris striata (Hutton) (p. 33)

A. Holotype, EC 136, ambulacral plates, 2·3 mm. Brighton, south-west Nelson—Duntroonian.

Phyllacanthus titan sp. nov. (p. 49)

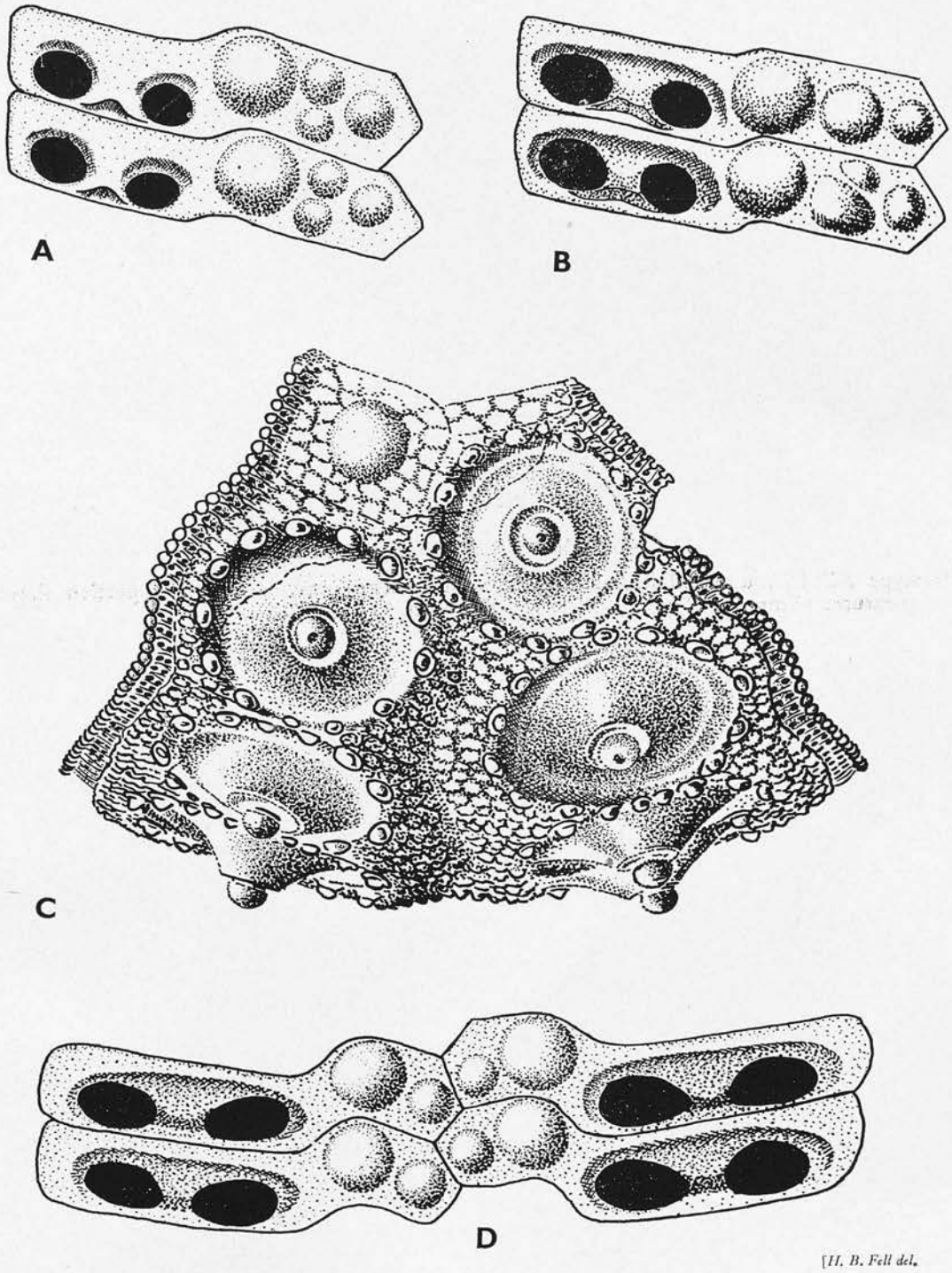
B. Ambulacral plates, 3 mm., paratype EC 104, uppermost Mount Brown beds, Weka Pass (zone F of Thomson)—Waiauan.

Phyllacanthus wellmanae sp. nov. (p. 51)

C. Holotype, EC 167, aboral aspect, 45 mm. GS 5832, Kapitean.

D. Holotype, EC 167, ambulacral plates of different part of test from that shown in C. 5 mm.

PLATE 1



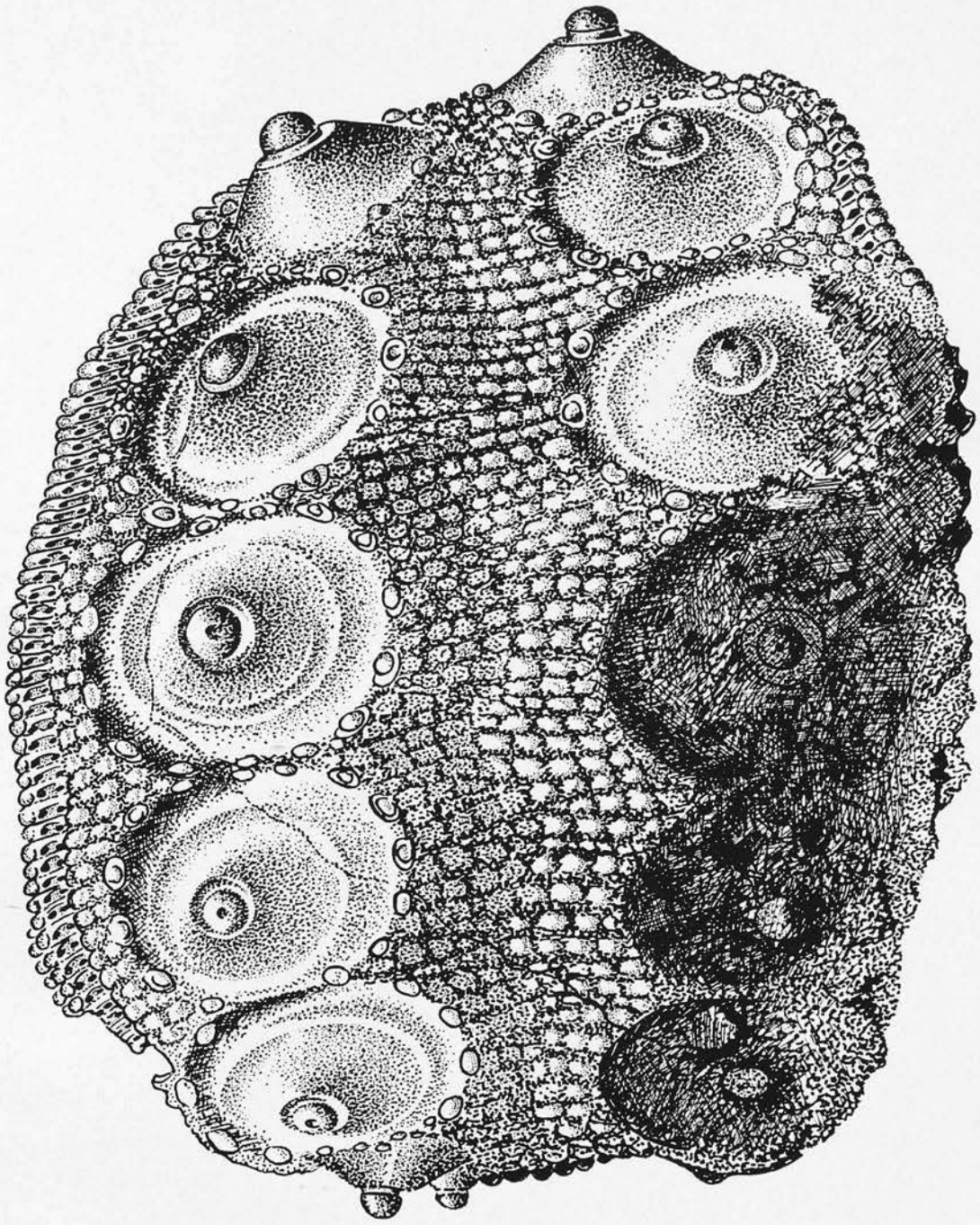
[*H. B. Fell del.*

PLATE 2

Phyllacanthus wellmanae sp. nov. (p. 51)

Holotype EC 167, interambulacral segment with attached ambulacra. The portion shown measures 45 mm. × 55 mm. GS 5832—Kapitean.

PLATE 2



H. B. Fell del.

PLATE 3

All specimens are in the collection of the New Zealand Geological Survey, whose registration numbers are cited. The major dimension of each is given.

Phyllacanthus titan sp. nov. (p. 49)

A. Apex of primary radiole, paratype EC 100. 6 mm. GS 3600—Waitakian.

B. Regenerating primary radiole, paratype EC 101. 38 mm. GS 172—Hutchinsonian.

C. Proximal fragment of large primary radiole, paratype EC 102. 20 mm. GS 172—Hutchinsonian.

D. Ambulacral plates, paratype EC 103. 3 mm. GS 74 (" Upper Mount Brown beds, Weka Pass ")—Duntroonian.

E. Interambulacral plate and associated ambulacrals, paratype EC 103. 19 mm. GS 74 (" Upper Mount Brown beds, Weka Pass ")—Duntroonian.

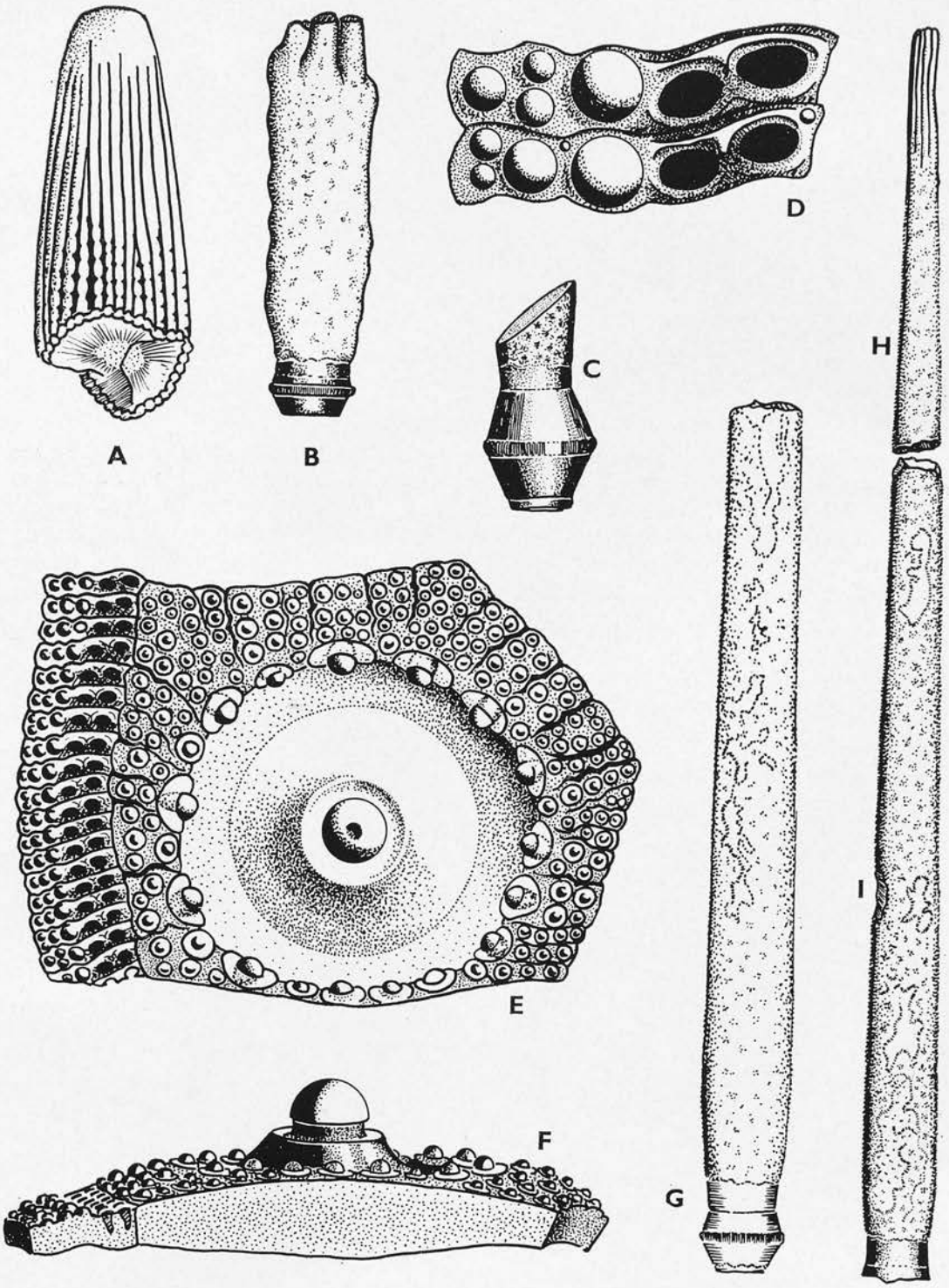
F. Profile of E.

G. Holotype, Primary radiole, EC 105. 81 mm. GS 172—Hutchinsonian.

H. Distal part of primary radiole, paratype EC 106. 40 mm. GS 172—Hutchinsonian.

I. Proximal part of primary radiole, approximately complementary to H above, paratype EC 107. 78 mm. GS 172—Hutchinsonian.

PLATE 3



[*H. B. Fell del.*

PLATE 4

Goniocidaris hebe sp. nov. (p. 37)

All specimens illustrated in this plate are from GS 311—Duntroonian–Waitakian—and are in the collection of the New Zealand Geological Survey, whose registration numbers are cited. The major dimension of each is given.

A. Apical cup-shaped primary radiole, paratype EC 108. 10 mm.

B. Primary radiole, paratype EC 109. 10 mm.

C. Holotype, primary radiole with lateral wings, EC 110. 17 mm.

D. Coronal tubercle with partial crenulation, paratype EC 111. 3 mm.

E. Primary radiole with terminal cup and spurs, paratype EC 112. 24 mm.

F. Interambulacral plate, probably adapical, paratype EC 113. 6·5 mm.

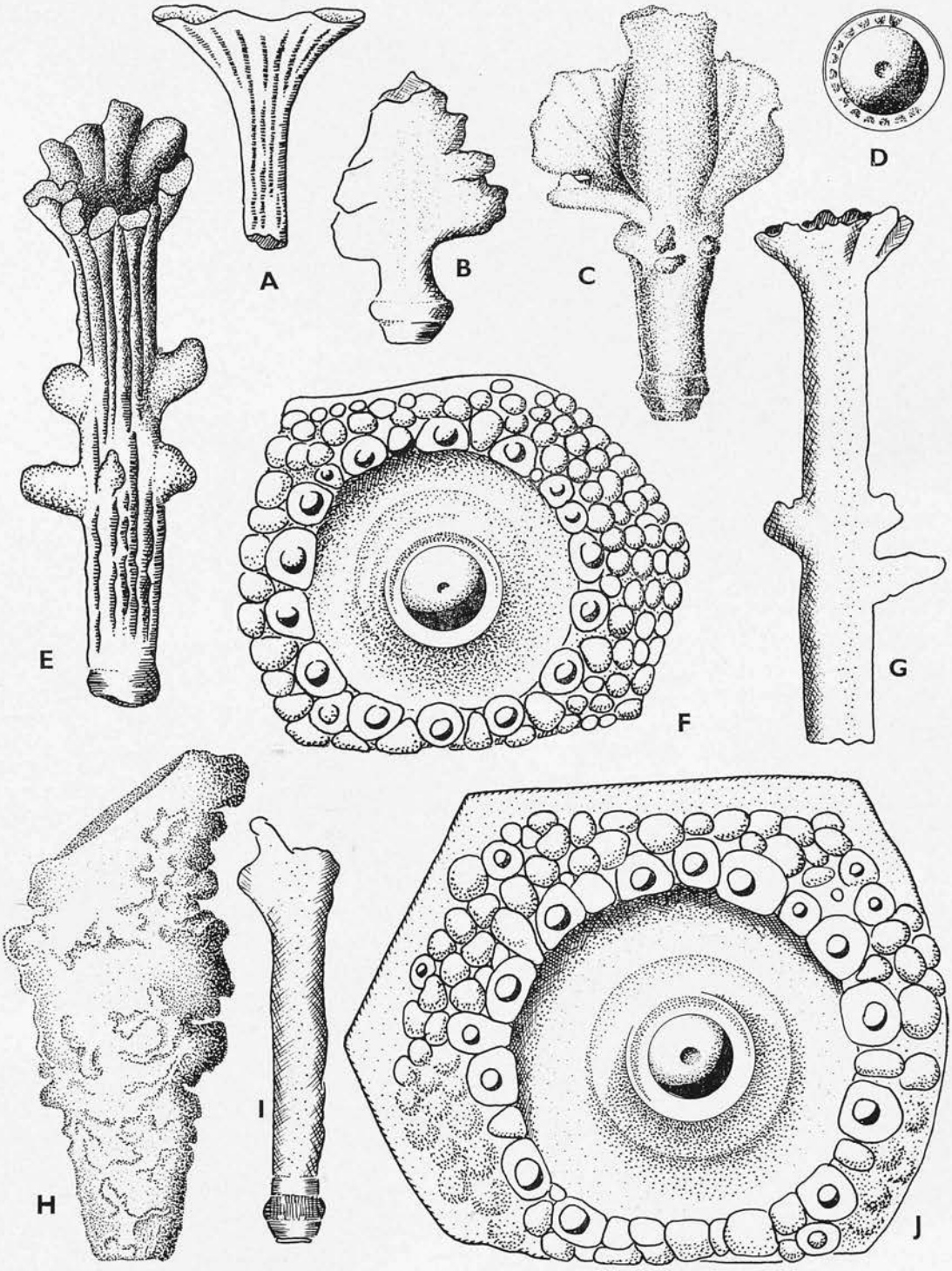
G. Primary radiole with terminal cup and spurs, paratype EC 114. 21·5 mm.

H. Primary radiole showing extreme flattening, paratype EC 115. 21 mm.

I. Small primary radiole, paratype EC 116. 17·5 mm.

J. Larger interambulacral plate, paratype EC 117. 8·5 mm.

PLATE 4



H. B. Fell del.

PLATE 5

The major dimension of each specimen is given.

Goniocidaris umbraculum Hutton (p. 40)

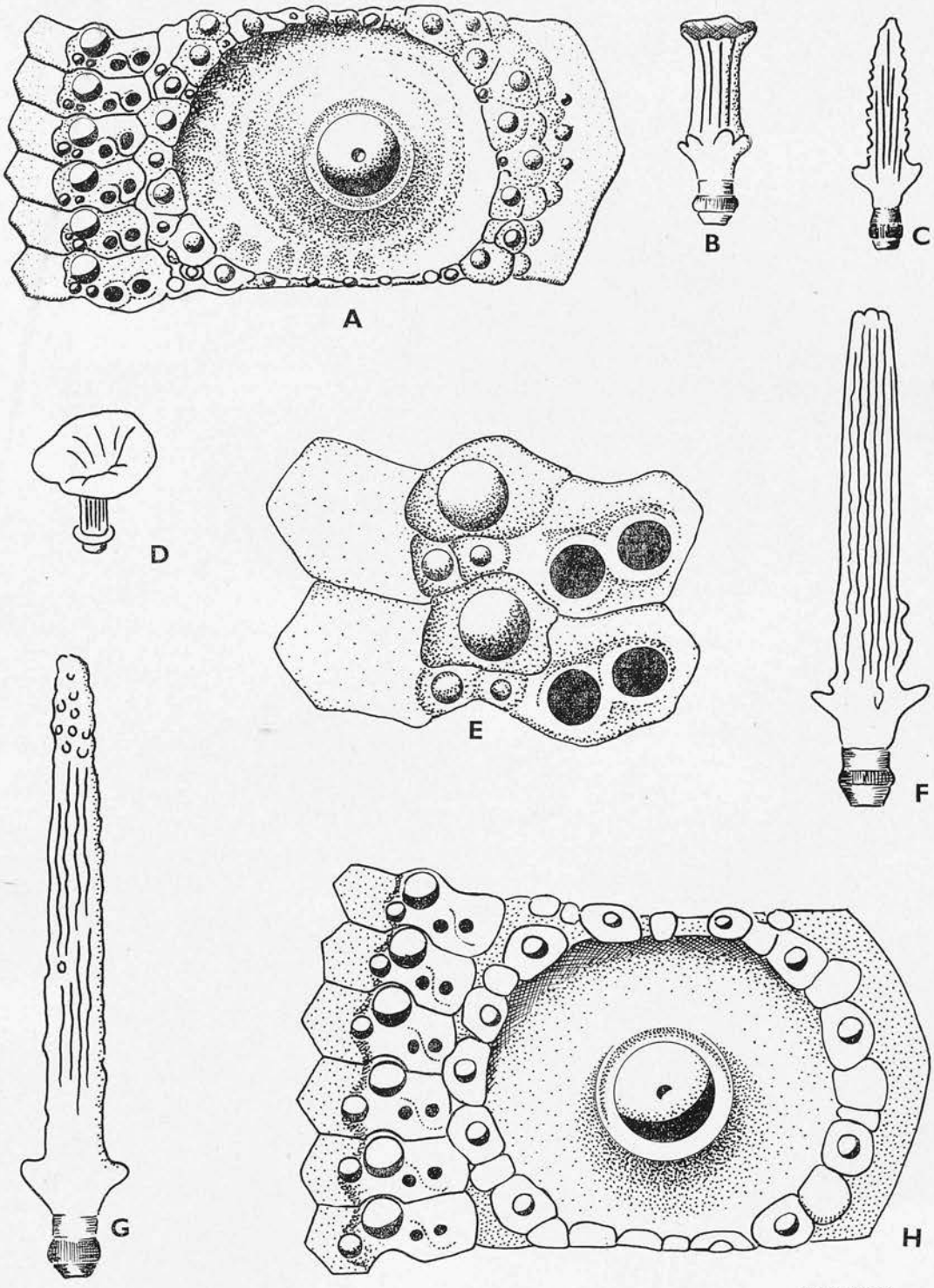
Recent specimens from Cook Strait, 50 fathoms; in the writer's collection.

A. Interambulacral plate and associated ambulacrals. 8·5 mm.
B. Adapical transitional type of primary radiole. 8·5 mm.
C. Adoral primary radiole. 10 mm.
D. Apical cup-shaped primary radiole. 6 mm.
E. Ambulacral ambital plates. 1·8 mm.
F. Ambital primary radiole. 21 mm.
G. Ambital primary radiole. 26 mm.

Goniocidaris pusilla sp. nov. (p. 39)

H. Holotype, Department of Geology, University of Otago. Interambulacral plate near ambitus, and associated ambulacrals. 4 mm. Black Head, Dunedin, Otago—Otaian.

PLATE 5



[*H. B. Fell del.*

PLATE 6

All specimens illustrated are in the collection of the New Zealand Geological Survey, whose registration numbers are cited. The major dimension of each is given.

Stereocidaris hutchinsoni sp. nov. (p. 35)

A. Primary radiole, paratype EC 118. 24 mm. GS 5752—Nukumaruan.

B. Holotype, EC 119. Ambulacral plates, 2·5 mm. GS 4259—lower Nukumaruan.

C. Proximal part of primary radiole, paratype EC 121. 16 mm. GS 5752—Nukumaruan.

D. Adoral primary radiole, paratype EC 122. 8·5 mm. GS 5752—Nukumaruan.

F. Small interambulacral plate (eroded), paratype EC 120. 5·5 mm. GS 5438—Nukumaruan.

G. H. Holotype, EC 119. Interambulacral plate and associated ambulacrals. 16 mm. GS 4259—Lower Nukumaruan.

J. Apical view of flattened primary radiole, paratype EC 125. 3 mm. GS 5752—Nukumaruan.

K. Lateral view of EC 125. 20 mm.

L. Large cylindrical primary radiole shaft, paratype EC 126. 28 mm. GS 5752—Nukumaruan.

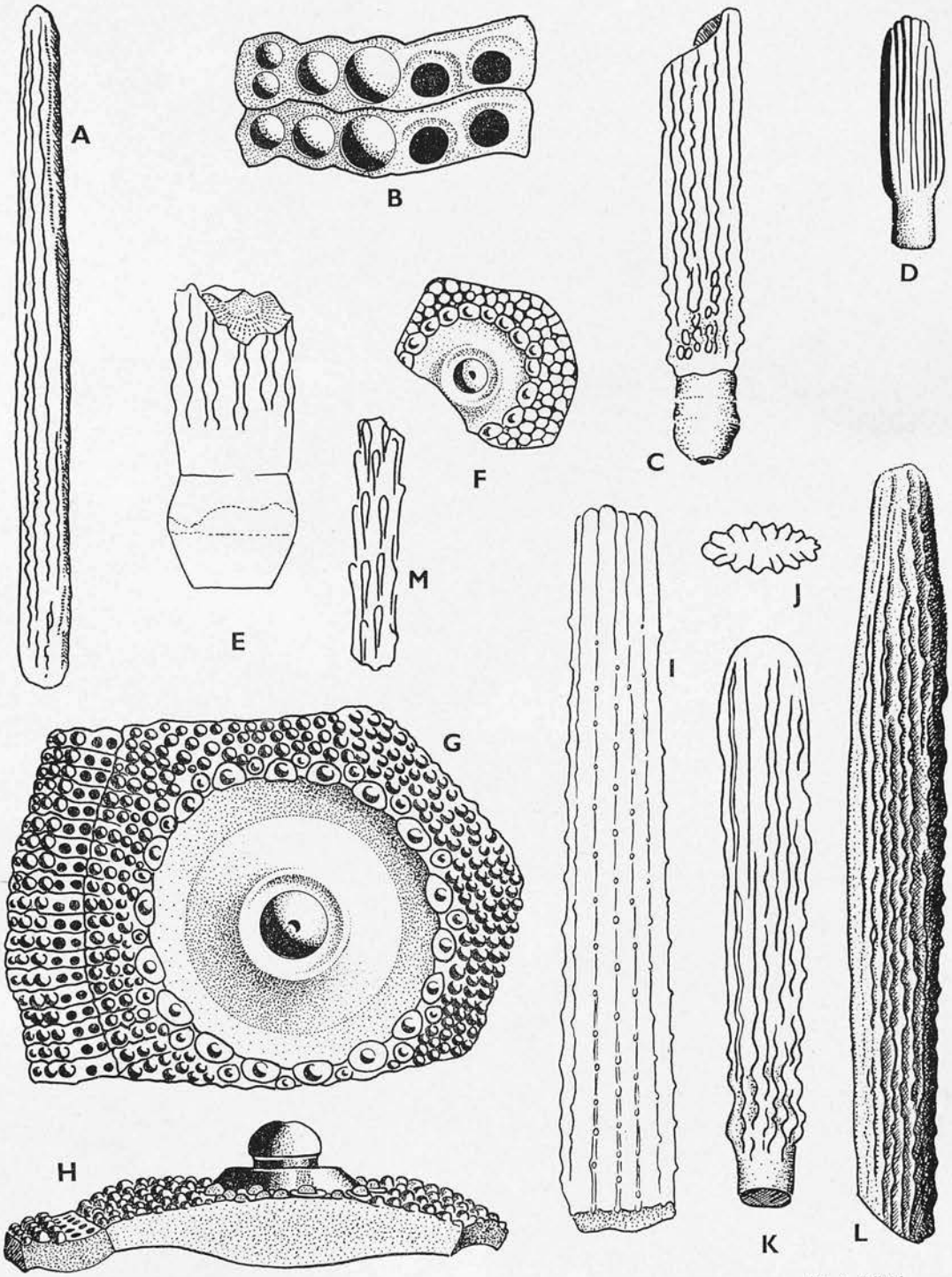
? *Stereocidaris striata* (Hutton) (p. 34)

E. Proximal part of primary radiole, specimen EC 123. 7·5 mm. GS 5516—Whaingaroan.

I. Distal part of shaft of primary radiole, specimen EC 124. 17·5 mm. GS 5516—Whaingaroan.

M. Distal part of shaft of primary radiole, specimen EC 163. 16 mm. GS 2225—Waitakian.

PLATE 6



[*H. B. Fell del.*

PLATE 7

The major dimension of each specimen is given.

Histocidaris mckayi sp. nov. (p. 30)

A. Holotype, third interambulacral plate from apical region. 12 mm. Department of Geology, University of Otago. Waihao Forks—Duntroonian.

C. Profile of A.

B. Ambulacral plates, paratype. 2·5 mm. Department of Geology, University of Otago. Kakanui—Waitakian.

E. Proximal view of base of primary radiole, restored from comparative study of various specimens. *ca* 3·5 mm.

G. Proximal part of primary radiole, paratype EC 127. 11 mm. GS 484—Waitakian.

I, J. Apical and lateral views, partly restored, of oral radiole from holotype. 2·5 and 13 mm.

Goniocidaris hebe sp. nov. (p. 37)

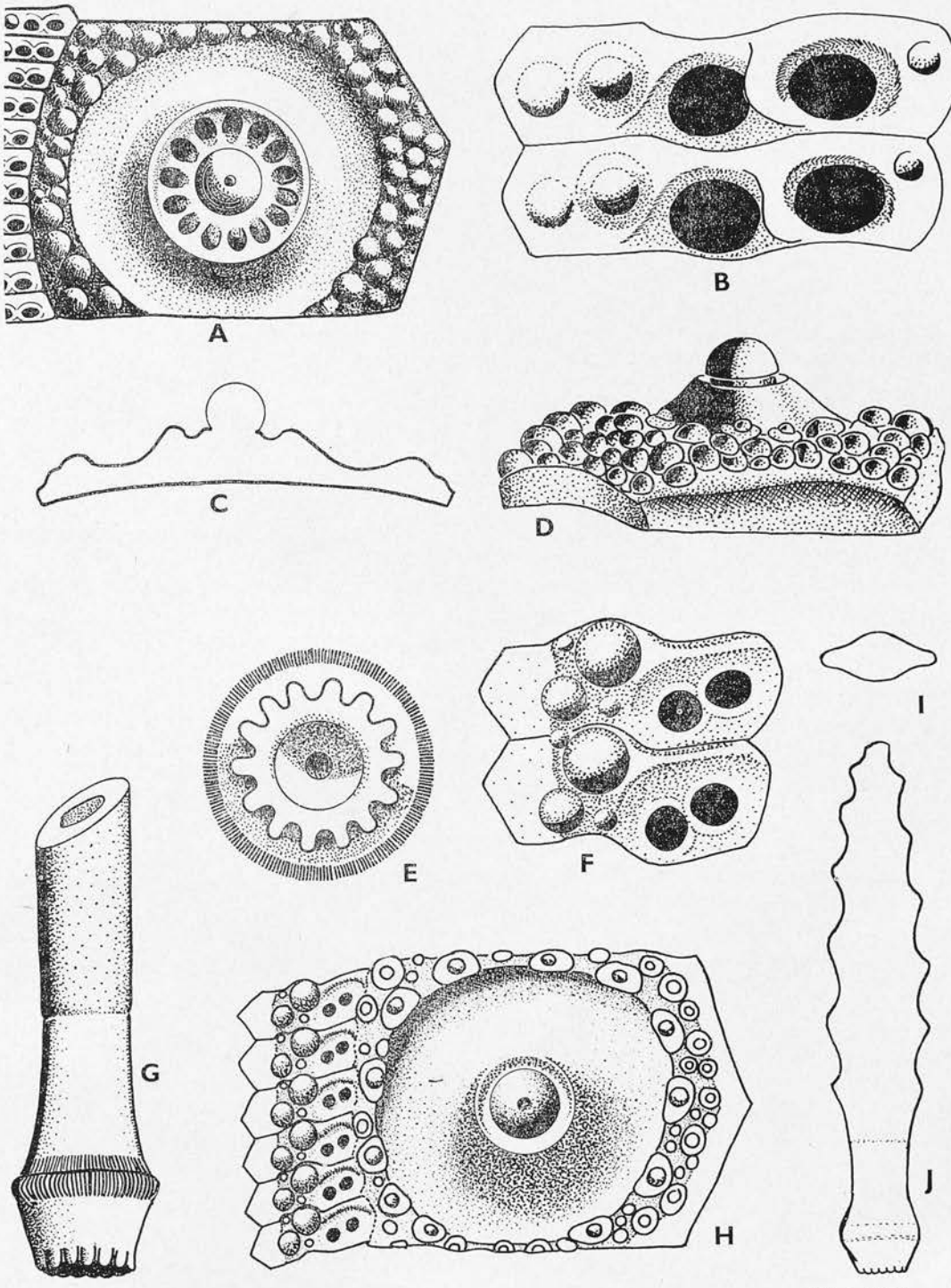
D. Profile view, from upper side, of interambulacral plate shown in Plate 4, F, paratype EC 113. 6·5 mm. GS 311—Duntroonian–Waitakian.

Ogmocidaris benhami Mortensen (p. 42)

F. Ambulacral plates. 1·3 mm. 70 fathoms, off Opotiki. In the writer's collection.

H. Ambital interambulacral plate with associated ambulacrals. 5·5 mm. Recent.

PLATE 7



[*H. B. Fell del.*

PLATE 8

All specimens illustrated are in the collection of the New Zealand Geological Survey, whose registration numbers are cited. The major dimension of each is given.

Eucidaris strobilata sp. nov. (p. 47)

A. Primary radiole, type four, paratype EC 128. 7 mm. GS 3600—Waitakian.

E. Holotype, EC 129. Primary radiole, type one, apical view of terminal crown and central prominence (and attached polyzoan). 4 mm. GS 1179—about Runangan–Whaingaroan.

F. Primary radiole, type two, paratype EC 131. 12 mm. GS 1179—about Runangan–Whaingaroan.

G, H. Primary radioles, type five, paratypes EC 130. 7 mm. and 3·5 mm. GS 3600—Waitakian.

J. Holotype, EC 129. Primary radiole, type one, lateral view of side with the larger warts (and attached polyzoan). 22 mm. GS 1179—about Runangan–Whaingaroan.

Prionocidaris marshalli sp. nov. (p. 54)

B. Primary radiole, paratype EC 134. 25 mm. Hampden—Bortonian.

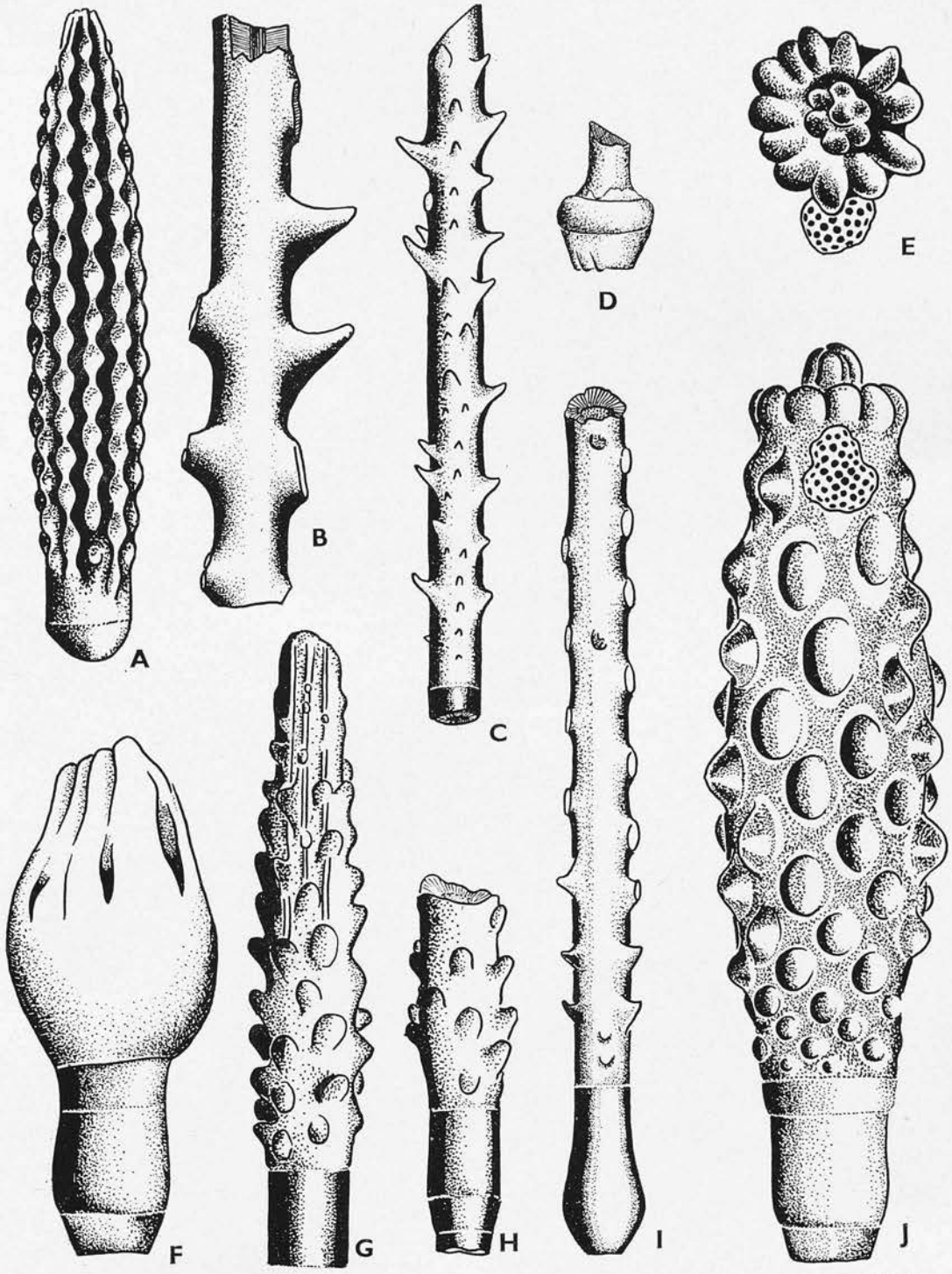
C. Primary radiole, paratype EC 135. 33 mm. Hampden—Bortonian.

I. Holotype, EC 133. Primary radiole, with collar and base. 40 mm. Hampden—Bortonian.

Goniocidaris hebe sp. nov. (p. 37)

D. Proximal part of primary radiole with abnormally swollen milled ring, paratype EC 132. 8 mm. GS 311—Duntroonian–Waitakian.

PLATE 8



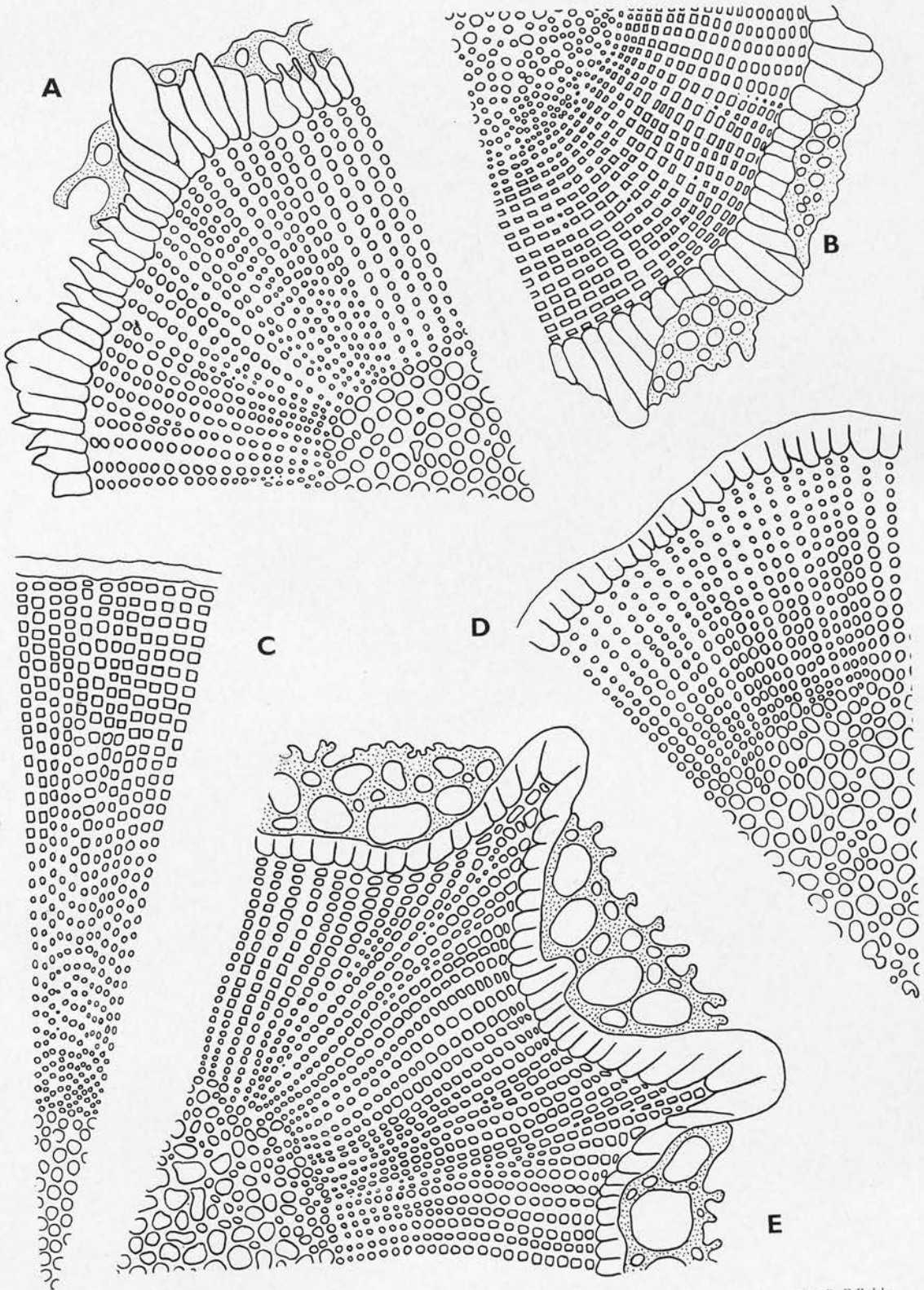
[*H. B. Fell del.*

PLATE 9

Transverse sections of primary radioles, ×75

A. ? *Stereocidaris striata* (Hutton) p. 34).
B. *Goniocidaris umbraculum* Hutton (p. 40)
C. *Prionocidaris marshalli* sp. nov. (p. 54).
D. *Histocidaris mckayi* sp. nov. (p. 30).
E. *Stereocidaris hutchinsoni* sp. nov. (p. 35).

PLATE 9



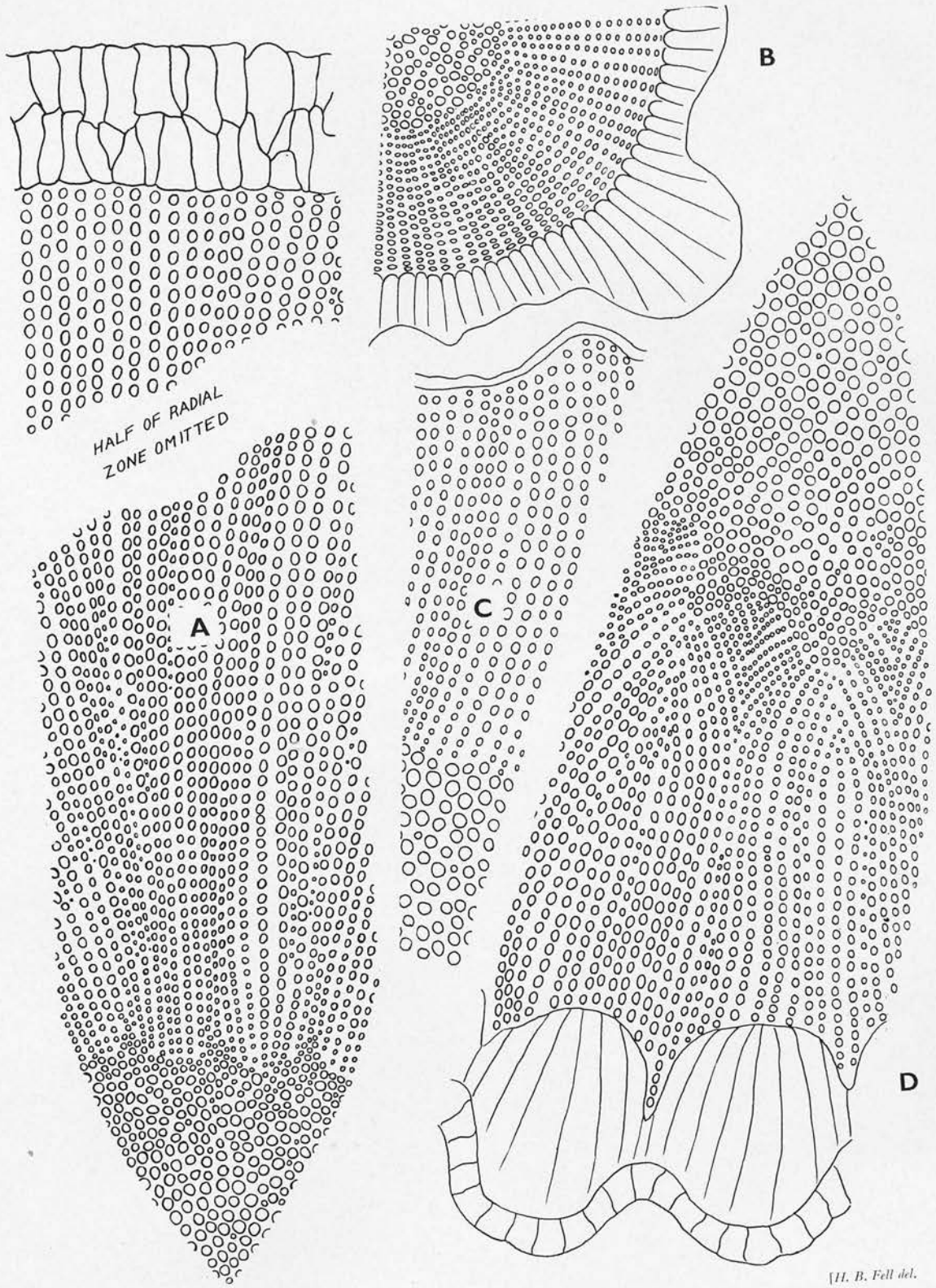
[H. B. Fell del.

PLATE 10

Transverse sections of primary radioles, ×75.

A. *Phyllacanthus titan* sp. nov., middle of shaft (p. 49).
B. *Eucidaris strobilata* sp. nov., radiole type four (p. 47).
C. *Prionocidaris haasti* sp. nov. (p. 54).
D. *Phyllacanthus titan* sp. nov., near apex (p. 49).

PLATE 10



[*H. B. Fell del.*

PLATE 11

Stereocidaris striata (Hutton) (p. 33)

A. Holotype, EC 136. Portion of test as seen from above, obliquely. The part visible measures 22 mm. in height. Brighton, south-west Nelson—Duntroonian.

Eucidaris coralloides sp. nov. (p. 46)

B. Holotype, EC 154. Primary radiole in lateral aspect. 19 mm. GS 5516—Whaingaroan.

C. Apical view of EC 154. Major diameter 13 mm.

Phyllacanthus titan sp. nov. (p. 49)

D. Holotype, EC 105, showing detail of proximal part of primary radiole. Diameter of milled ring 7 mm. GS 172—Hutchinsonian.

Eucidaris strobilata sp. nov. (p. 47)

E. Transverse section of primary radiole, type one, through shaft. The inner part of the section has been drawn so as to overlap upon the outer part. ×75.

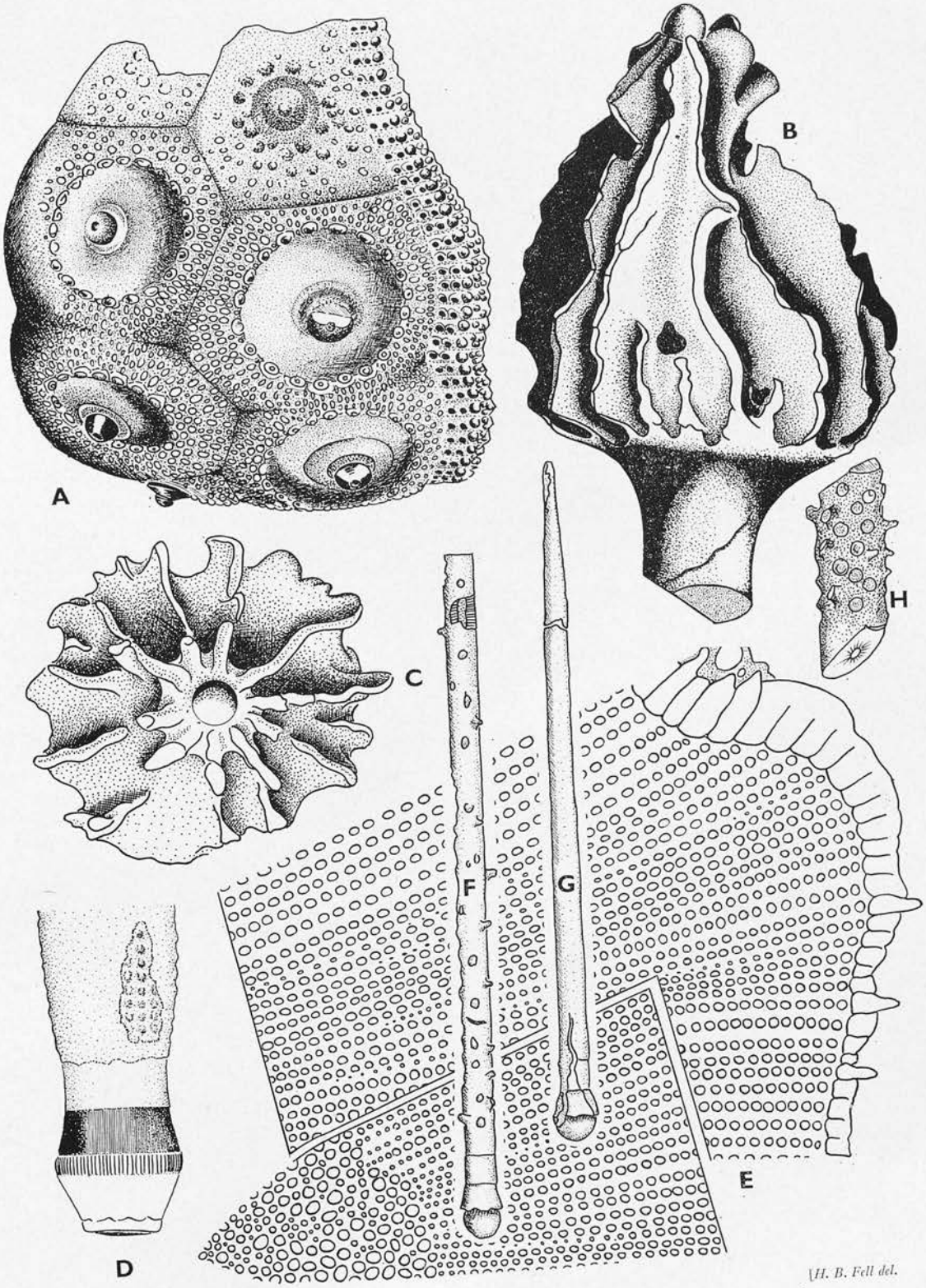
Prionocidaris haasti sp. nov. (p. 54)

F. Holotype, EC 161. Primary radiole. 58 mm. GS 74—Duntroonian.

G. Paratype, EC 161/A (embedded in same piece of matrix as holotype). 58 mm. GS 74—Duntroonian.

H. Paratype, EC 162, portion of large primary radiole. 17·5 mm. GS 5667—Otaian.

PLATE 11



[H. B. Fell del.

PLATE 12

Goniocidaris umbraculum Hutton (p. 40)

Three views of Recent specimen with radioles intact, *ca.* 45 mm. × 22 mm., overall measurements. Cook Strait, 50 fathoms; in the writer's collection.

A. Lateral aspect.

E. Aboral aspect.

F. Adoral aspect.

Ogmocidaris benhami Mortensen (p. 42)

Three views of Recent specimen with radioles intact, *ca.* 100 mm. × 35 mm. overall measurements. Off Cape Kidnappers, 200 fathoms, on grey-green mud; in the writer's collection.

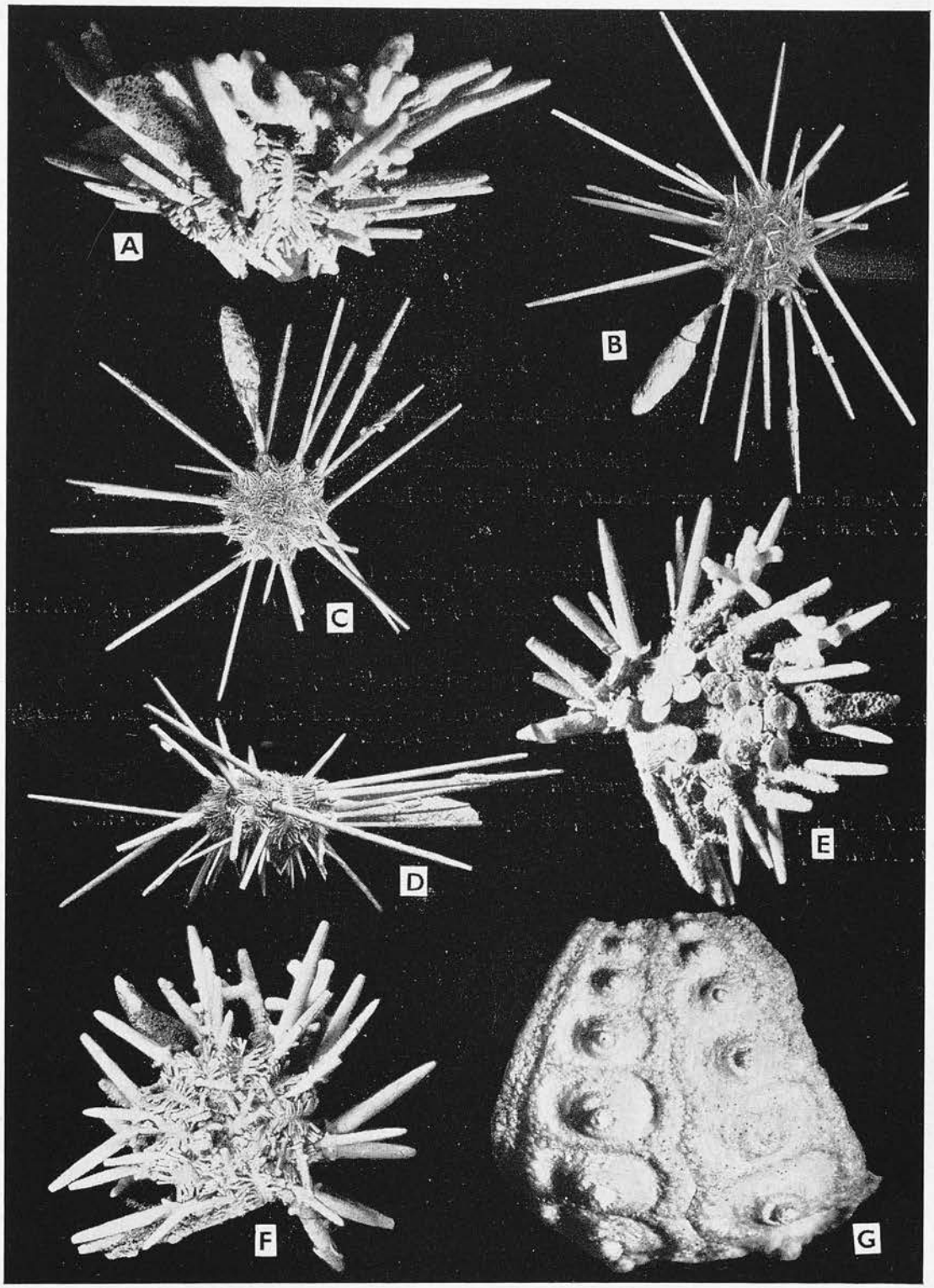
B. Adoral aspect.

C. Aboral aspect.

D. Lateral aspect.

Histocidaris mckayi sp. nov. (p. 30)

G. Adoral portion of interambulacrum, paratype from Waihao Limestone—Duntroonian. Major dimension of the portion visible, 26 mm.



[*Photo, J. T. Salmon*

PLATE 13

The major dimension is given.

Goniocidaris umbraculum Hutton (p. 40)

A. Aboral aspect. 22 mm. Recent, Cook Strait, 50 fathoms; in the writer's collection.
B. Adoral aspect of A.

Histocidaris mckayi sp. nov. (p. 30)

C. Holotype, aboral aspect. 47 mm. University of Otago, Department of Geology. Waihao Forks—Duntroonian.

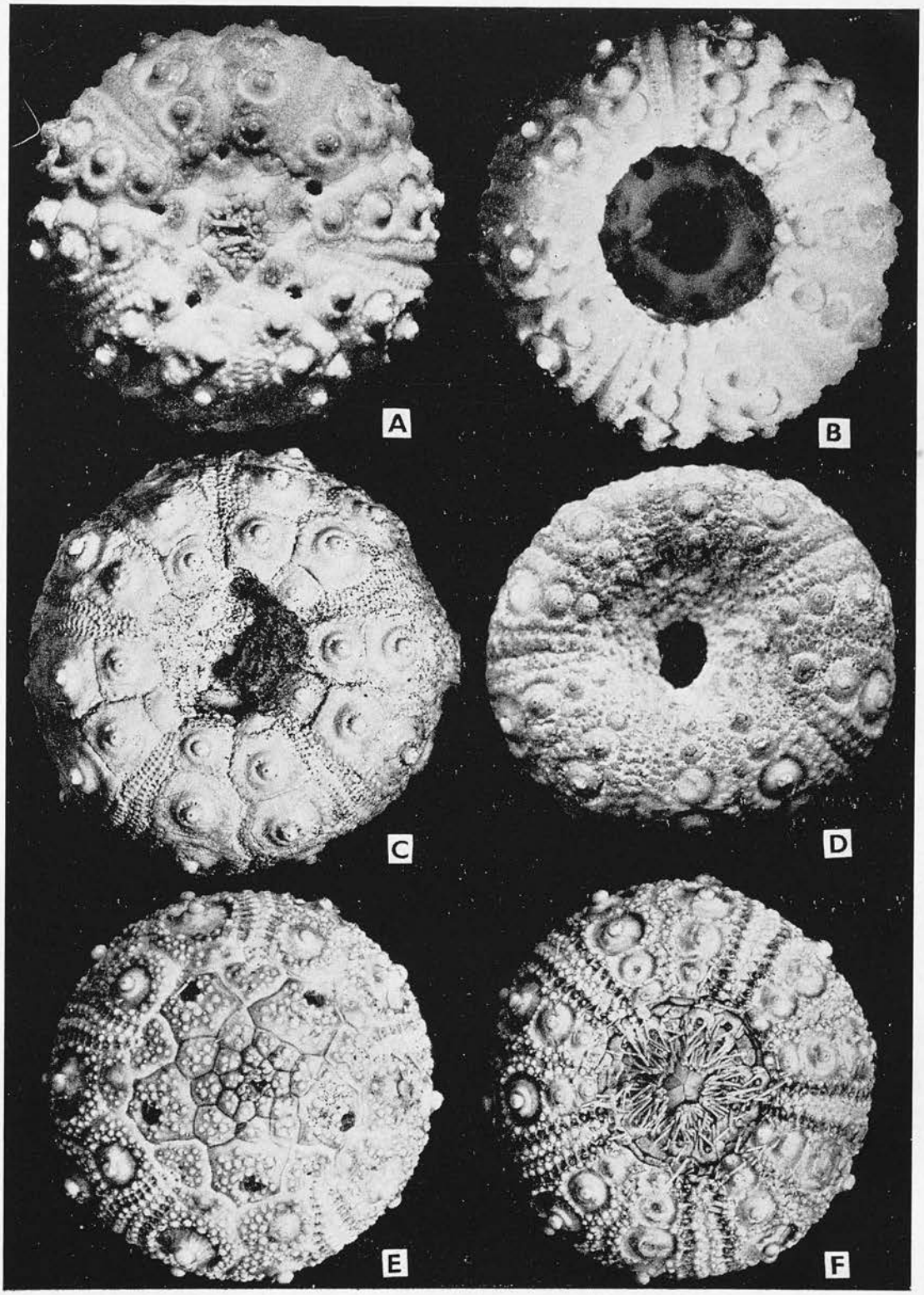
Goniocidaris pusilla sp. nov. (p. 39)

D. Adoral aspect of paratype in Department of Geology, University of Otago. 13 mm. Probably from one mile south of Shag Point, Otago—Otaian.

Ogmocidaris benhami Mortensen (p. 42)

E. Aboral aspect. 16 mm. Recent, off Opotiki, 70 fathoms; in the writer's collection.
F. Adoral aspect of E.

PLATE 13



[*Photo, J. T. Salmon*

PLATE 14

The major dimension is given.

Goniocidaris umbraculum Hutton (p. 40)

A. Lateral aspect, 22 mm. Recent, Cook Strait, 50 fathoms; in the writer's collection.

Ogmocidaris benhami Mortensen (p. 42)

B. Lateral aspect, 16 mm. Recent, off Opotiki, 70 fathoms; in the writer's collection.

Goniocidaris pusilla sp. nov. (p. 39)

C. Lateral aspect, paratype, 13 mm.; probably from 1 mile south of Shag Point. Geology Department, University of Otago—Otaian.

Stereocidaris striata (Hutton) (p. 33)

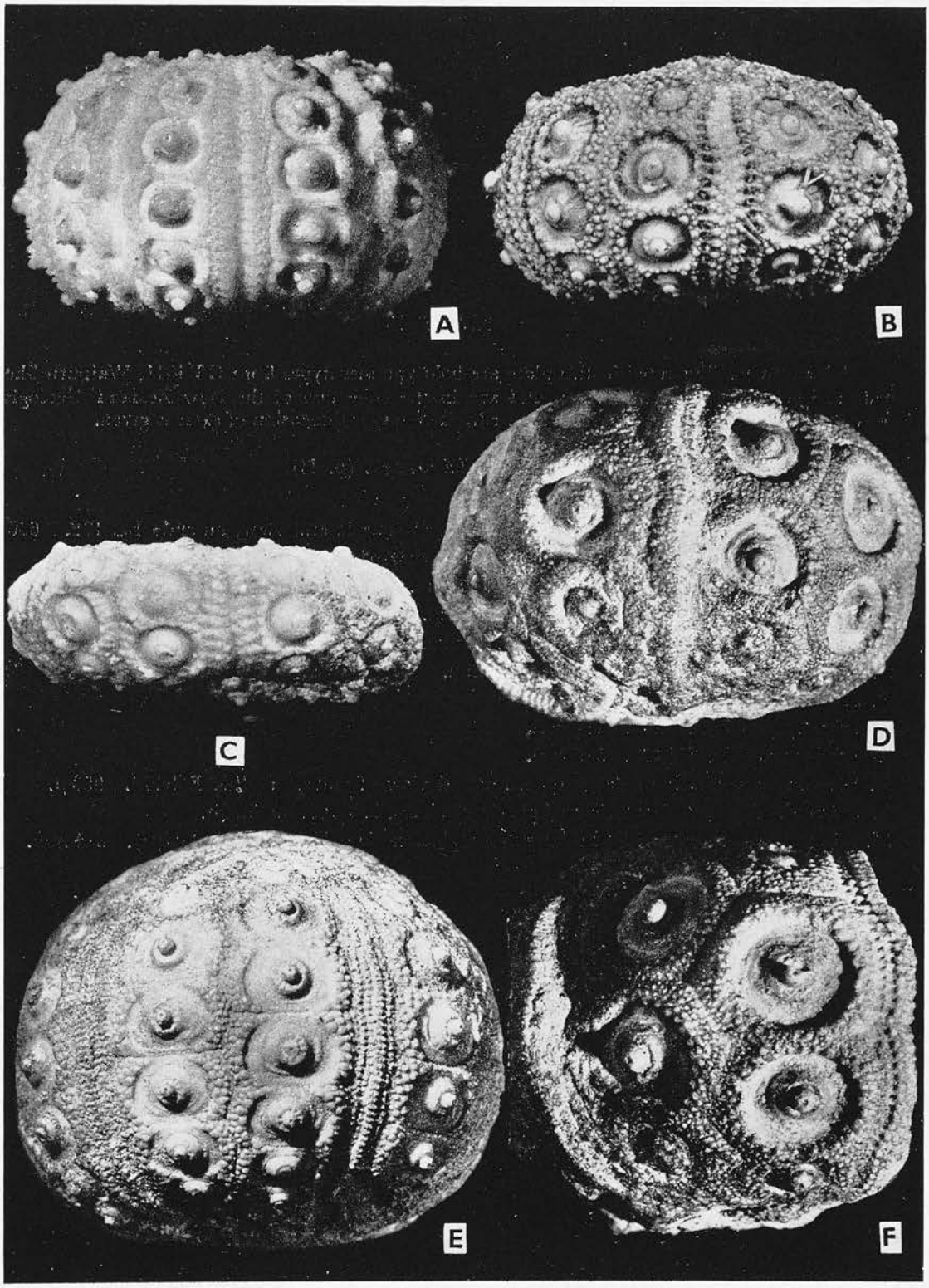
D. Holotype, ambulacral lateral aspect, 37 mm. Brighton, south-west Nelson. Specimen EC 136 in the collection of the New Zealand Geological Survey—Duntroonian.

F. Interambulacral aspect of EC 136; height in this view *ca* 24 mm. Note rudimentary areole on right upper plate.

Histocidaris mckayi sp. nov. (p. 30)

E. Portion of test, lateral aspect, 58 mm. Paratype EC 137. GS 432—Duntroonian.

PLATE 14



[*Photo, J. T. Salmon*

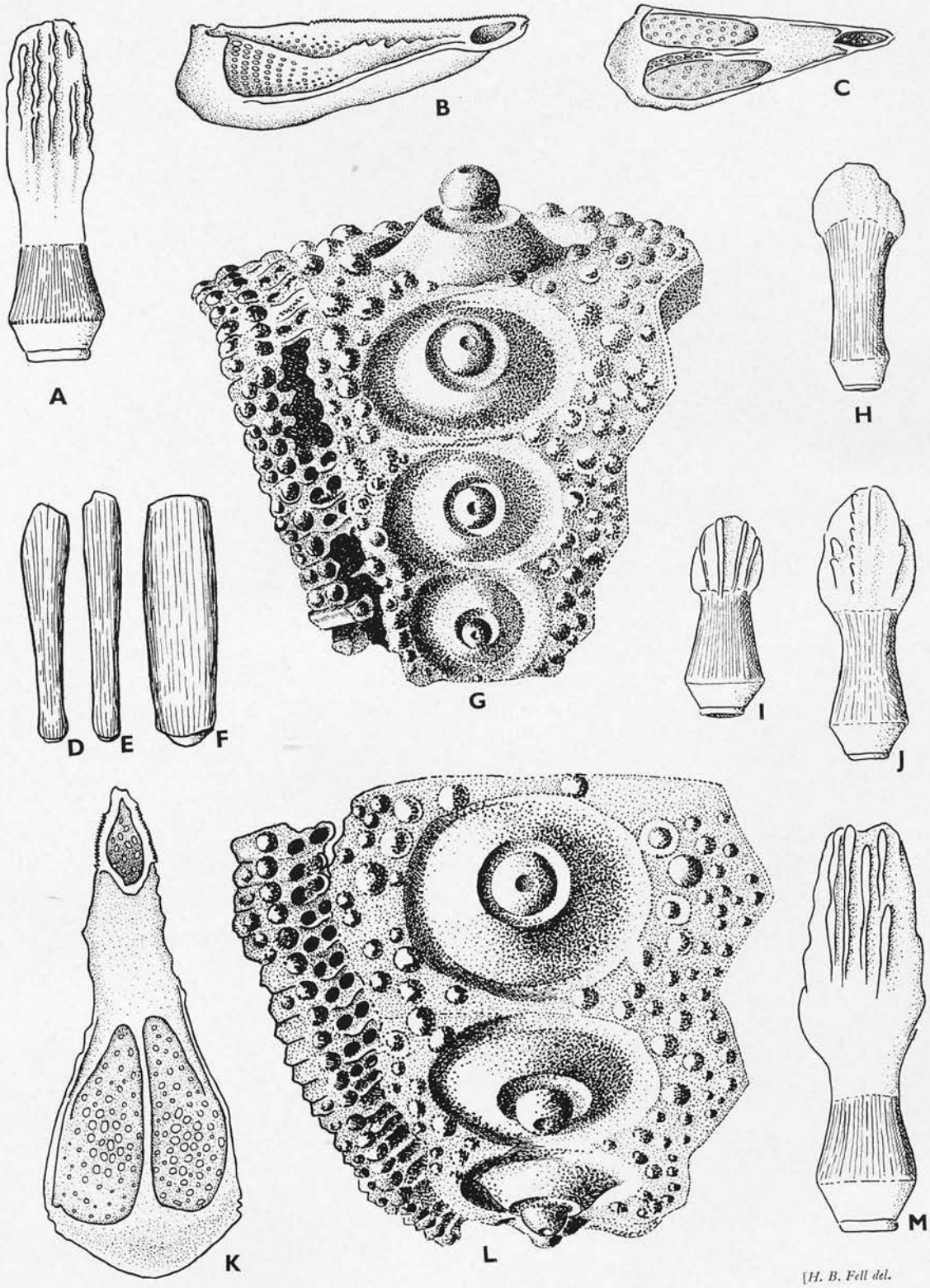
PLATE 15

All specimens illustrated in this plate are holotype merotypes from GS 4011, Waipuru Shell-bed, Kai-iwi Valley—Nukumaruan, and are in the collection of the New Zealand Geological Survey, whose registration numbers are cited. The major dimension of each is given.

Notocidaris vellai sp. nov. (p. 43)

A. Primary radiole, EC 173. 7·0 mm.
B. Globiferous pedicellaria of intermediate size, oblique lateral view, on slide EC 178. 600 μ.
C. Globiferous pedicellaria, small type, internal view of valve, on slide EC 178. 480 μ.
D. Club-shaped secondary radiole, EC 175. 3 mm.
E. Cylindrical secondary radiole, EC 176. 3 mm.
F. Scrobicular secondary radiole, EC 177. 3 mm.
G. Segment of test, oral view, EC 169. 11 mm.
H. Primary radiole, EC 171. 4·8 mm.
I. Primary radiole, EC 170. 4·1 mm.
J. Primary radiole, EC 172. 5·6 mm.
K. Globiferous pedicellaria, large type, internal view of valve, on slide EC 178. 850 μ.
L. Segment of test, ambital view of proximal plates, EC 169. 9·5 mm.
M. Primary radiole, EC 174 (the largest complete radiole found with holotype). 8·4 mm.

PLATE 15



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